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NON-BREEDING ECOLOGY OF DIVING DUCKS IN SOUTHERNMOST SWEDEN

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This thesis consists of the following papers:

- I. The wintering populations of diving ducks in Scania.
- II. Habitat selection, food choice and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season.
- III. Habitat selection, food choice and food consumption of diving ducks on a south Swedish lake.
- IV. Food consumption of diving ducks wintering at the coast of south Sweden in relation to food resources. - *Oikos* 1969:128-135.
- V. Food-seeking activity of south Swedish diving ducks in the non-breeding season. - *Oikos* 1970 in press.
- VI. Local and seasonal variations in sex-ratios of diving ducks in south Sweden during the non-breeding season. - *Ornis Scandinavica* 1970 in press.

Background

During the last ten to fifteen years a large body of data concerning the winter distribution, seasonal fluctuations in numbers and trends in duck populations has been gathered in various European countries under the scheme of the International Wildfowl Counts. In Sweden such counts were started in 1959 and during the winter 1962/63 a count programme was started in the southernmost province of the country, Scania.

As only little information concerning various aspects of the non-breeding ecology of diving ducks was available in the literature the study was extended to a survey of the non-breeding ecology of these species in 1964/65.

General summary

The results are summarized in the abstracts preceeding the various papers so only a short general summary of the most important findings will be given here.

Scania was found to be the most important winter area in Sweden for diving ducks with a population (excluding *Clangula hyemalis* and *Melanitta*) of between 19,200 and 35,700 in mid-January. Annual fluctuations were found in most species in relation to the severity of the winter but in two common species, *Aythya fuligula* and *Mergus merganser*, a significant increase occurred during the study period.

The available food resources both in coastal areas and in the lake studied were sufficient for larger numbers of ducks than were in fact using these areas.

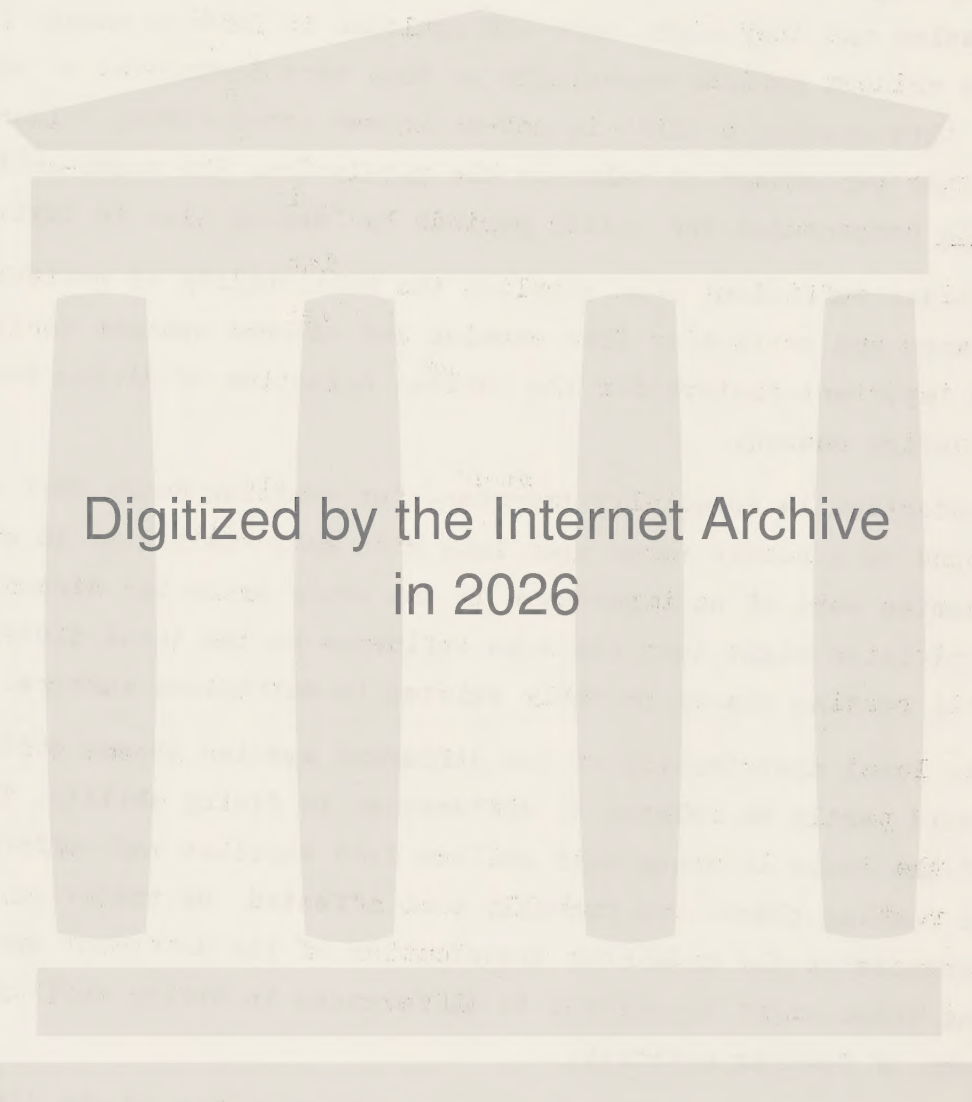
However, the food situation might even so be critical during hard periods, when ice makes it impossible to utilize food resources in areas accessible in milder periods. The effect of ice is strengthened by the fact that the shallow areas where diving is most economic are the first to freeze. Increased food-seeking intensity during cold periods was found and in Bucephala clangula a significant correlation was found between increased food-seeking intensity and decreasing temperatures. This species showed very high feeding intensities during cold periods especially in the smaller females and they might have difficulties in finding enough food during the coldest periods especially as they were restricted to daytime feeding. In this species a shift in sex-ratio was noted during colder periods to a higher percentage of males in the population. The night-active Aythya fuligula compensated the colder periods by feeding also in daytime.

Besides sufficient food supplies the availability of suitable resting places and protection from enemies and adverse weather conditions might be important factors for the habitat selection of diving ducks in non-breeding season.

Protection is especially important for moulting ducks that were also found on a rather large open lake with good visibility in all directions. Enemies were of no importance in the study areas but disturbance from human activities might have had some influence on the local distribution. Suitable resting places probably existed in sufficient numbers.

The local distribution of the different species showed differences that could partly be related to differences in diving ability. The distribution of the ducks in areas with uniform food supplies and sufficient numbers of resting places was probably much affected by tradition. Regional differences in the midwinter distribution of the different species were found and these might be related to differences in diving ability and the pattern of feeding activity.

In both coastal and inland areas the food choice of the different species was rather similar as was to be expected in areas with superabundant food. However, some differences were found between most species with regard to secondary food items.



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The wintering populations of diving ducks in Scania

Abstract

Counts of non-breeding diving ducks were started along the coasts of Scania in 1962/63 and later extended. The dominant species were Aythya fuligula, Bucephala clangula, Clangula hyemalis, and Mergus merganser, but all Swedish diving ducks were found in the areas. In most species, a movement away from the inland areas was found when the lakes froze whereas an inland movement in spring occurred as soon as the lakes were free of ice. During the winter, fluctuations in relation to the weather and ice situation was found.

The midwinter population in Scania excluding C. hyemalis and the Melanitta species which stayed too far out to sea to be counted, varied between 19,200 and 35,700. Annual indices showed fluctuations in the wintering populations and a significant increase was found for A. fuligula and M. merganser and in the sparse species M. serrator and Somateria mollissima. B. clangula showed high indices during cold winters.

Regional differences in the composition of the diving duck populations occurred between different parts of the Baltic that might be related to different aspects of the feeding ecology such as diving ability and activity type.

1. Introduction

During the last ten to fifteen years a large amount of work has been carried out under the scheme of the International Wildfowl Counts to determine the size and composition of the duck populations of various European countries and to follow the annual and seasonal variations in their numbers (cf. e.g. Atkinson-Willes 1963, 1969, Geroudet 1969, Isakov 1968, Joensen 1968, Leuzinger 1969, Nilsson 1968 a, 1968 b, Requate 1954, Roux & Tamasier 1969, Rutschke 1969). These studies were planned to assess the situation in whole countries but as they had to rely mainly on voluntary helpers it was not possible to determine the size of the winter population in more than a few countries (Atkinson-Willes 1963, Joensen 1968, Leuzinger 1969) or some smaller areas (Nehls 1963, 1967, 1968 a, 1968 b, 1969, Nilsson 1967 b, Szijj 1963). The trends in the wintering populations of a whole country has as yet only been published for Great Britain (Atkinson-Willes & Frith 1965) but data from one important locality in Germany were published by Szijj (1963). In the last four years a vast amount of data has been gathered on the midwinter distribution and composition of the European

waterfowl populations under the scheme of the International Wildfowl Research Bureau's Duck Working Group ("The International Midwinter Count") (cf. Atkinson-Willes 1969).

Counts were started in Scania in 1962/63 (and later extended) in order to elucidate the factors affecting the choice of the area for wintering by diving ducks and the factors affecting the movements in and out of the area by these species. Moreover the counts were intended to provide data on the size and annual fluctuations in numbers of the diving duck populations of the area.

2. Study areas

The main work was undertaken in three study areas in SW Scania (Fig. 1) but one more extensive count each winter (the "midwinter count") covered almost the whole coast of the province. Two of the study areas were situated on the coasts: Öresund from Vikhög to Klagshamn and the south coast between Ystad and Kämpinge. The third area comprised several lakes in SW Scania. In 1968/69 and 1969/70 some counts were also made on Lake Ringsjön in central Scania.

The two marine areas will be described in detail elsewhere. Both are characterized by extensive shallow areas, especially in the Öresund, with rich food supplies for diving ducks.

The lakes all belong to the eutrophic type but are of somewhat different appearance. Lake Krankesjön and Lake Björkesåkrasjön have rich emergent vegetation, mainly Phragmites, whereas the other lakes have much less emergent vegetation. Lake Häckebergasjön and Lake Fjällfotasjön are entirely surrounded by woods whereas the other lakes are situated in more or less open country. *

3. General weather characteristics

The periods of ice-coverage in the study areas in 1964/65-1967/68 are found in the diagrams on the seasonal fluctuations in number of the different species and weekly mean temperatures at Malmö are shown in Fig. 4. The lakes were ice-covered for considerable periods every winter. The coastal areas have sometimes been covered with ice but as the ice drifted open water has generally been available, at least in some places.

The winter of 1962/63 was very hard in most parts of Europe. Lommabukten, the only coastal area studied, was completely frozen in January-February with only two small areas open. The lakes were frozen from mid December to late March.

In 1963/64 the winter was much milder and Lommabukten was free of ice the whole winter. The lakes were frozen from late December to March.

1964/65 had also a fairly mild winter but a cold period occurred in March, when ice formed in the Öresund.

1965/66 was cold with a hard frost period in the second week of November and the lakes freezing by that time. Extensive ice formed along the coasts but it was generally drifting and thus some open areas were always available. In the spring there was a cold period in mid April.

1966/67 was mild throughout the winter and no ice formed along the coasts.

The winter of 1967/68 was mild for most periods but a cold period occurred from the last week of December to mid January when most parts of the Öresund and the south coast were covered with ice. February was mild and the lakes were then open for a few days.

1968/69 had a normal winter with no ice in the coastal areas except near the shore. The lakes were frozen from mid December to mid March.

In 1969/70 the winter was hard with most parts of the coastal areas ice-covered from the first days of February till late March. The ice coverage was heavy in the rest of the country and the spring was late. The lakes were frozen from November till after mid April.

4. Collecting and evaluating the observation data

Methods and errors in the field counts

Counts were made regularly from mid September to mid April, in general at least twice a month in the three study areas; the counts on the south coast were however not started until October in the first two years. The counts in the Öresund which started in September 1962 were confined to Lommabukten but were extended in October 1964 to cover the whole area between Vikhög and Klagshamn. The counts on the south coast started in October 1964 and the counts in the lake area in March 1965. Midwinter counts covering the whole coast of Scania in mid January were first made in 1964. - In 1968/69 and 1969/70 only monthly counts were made.

The counts in the study areas were all made by me following a standard procedure. Each area was divided into sectors that were counted separately from fixed observation posts so that the whole area between the posts could be counted accurately by telescope (40 x 60). In the lake area each lake was a counting unit. One study area was covered in one day. When counting larger concentrations a tape recorder was used. Counts were

only made during favourable weather conditions, i.e. fairly calm weather and good visibility. Greatest possible care was taken when counting diving flocks to avoid double counting or too low counts. Each such flock was generally counted twice, often after disturbing the birds so as to prevent them from diving.

The "midwinter counts" were made by me with the aid of voluntary helpers. The coast was divided into sectors taking prominent topographical features as borders. Each observer counted one or more sectors, nearly all counts being made in one day. In general the different sectors were counted by the same observer each year.

The factors affecting the reliability of duck counts in both coastal and inland waters have been discussed in some reports from the International Wildfowl Counts (cf. Leuzinger 1964, Nilsson 1967 b). They may be grouped in factors related to the local distribution and activity patterns of the different species and in counting errors.

On the coasts of Scania the Long-tailed Duck, Clangula hyemalis (L.), the Velvet Scoter, Melanitta fusca (L.), and the Common Scoter, Melanitta nigra (L.), often stay far out at sea and an observer on the shore will in most cases only see single specimens of the Scoters and a varying proportion of the Long-tailed Ducks. In the other species it was, in general, possible to see all individuals from the shore. In all species almost all individuals were stationary during the day unless disturbed, so that movements of the ducks were of no importance for the results of the counts.

Among the inshore species counting errors will affect counts made on large resting flocks, mainly Tufted Ducks, Aythya fuligula (L.), and counts made on dense concentrations of smaller diving groups, mainly Goldeneyes, Bucephala clangula (L.). By making repeated counts of resting flocks of Tufted Ducks an error of $\pm 10\%$ was estimated for flocks of up to 1,000 individuals but in the larger flocks of up to 5,000 individuals the error was about $\pm 20\%$. Counts on many small groups of Goldeneyes made in the short dive-pauses of each group were affected by an error of up to $\pm 20\%$ as estimated from comparisons between such counts and counts of Goldeneyes after they had been disturbed to prevent them from diving.

The lakes in the lake area are small and the diving ducks resting here could be easily seen as they normally stayed on the open water. The flocks were generally small and easy to count except in the Goosander, Mergus merganser L., that was sometimes seen diving in large compact flocks.

Estimation of the mean error in the counts

A marked variation was found between the counts on different days (Figs. 5-13) caused mainly by real changes in the wintering populations but part of this variation was certainly due to errors affecting the counts as discussed above. This error component will be largely constant for various intervals between counts as long as they are made in the same manner by the same observer and the ducks are not too concentrated, whereas the deviations between counts caused by real changes in the populations generally will be larger for longer intervals. This provides a method of estimating the maximum error affecting the counts of the different species.

For all species occurring in sufficiently large numbers the percentage change in numbers for whole study areas between counts on day 0 and after $0 + X$ days was calculated. The arithmetic means of these percentages were calculated for five-day periods of X and illustrated graphically (Fig. 2). The curves will show somewhat different appearance for the different species but an increase in the mean percentage change was found in all species. For short intervals between counts this increase was slight in some species. Extrapolation to the intersection with the ordinate will give an estimate of the maximum mean error affecting the counts. Only days with more than 50 individuals were used as day 0.

In the Scaup and Tufted Duck this method lead to an estimated error of about 20 %. In the Goldeneye the estimated error was 20-25 % for the south coast, and 25-30 % for the Öresund area. This was consistent with the distribution of the species in the two study areas, the Goldeneyes staying further from the shore in the Öresund area making the counts more difficult here than on the south coast. In the other species it was not possible to obtain a sufficient number of comparisons to use this method.

From the curves it is seen that after one month, the normal period between the International Wildfowl Counts, the mean change between counts exceeded the double estimated error, whereas no species reached this level after 15 days.

Most variation was in both + and - directions and when the algebraic means of the changes were calculated, instead of the arithmetic means, most variation tended to cancel out (Table 1). The counts may therefore be considered reliable in a series of counts even if the individual counts suffer from some errors.

Monthly counts as measures of changes in the diving duck populations

In the International Wildfowl Counts monthly intervals were chosen for practical reasons. Shorter intervals were considered to involve too much work for the voluntary helpers in relation to the gain in exactness, while longer intervals would give no indication of the seasonal fluctuations.

The mean of a series of counts in a certain period might be considered as the best estimate of the general population level in that period if most errors are at random in both + and - directions and thus mainly cancel one another out. When comparing the monthly means with the counts obtained on the International Wildfowl Count dates (Table 2) a marked tendency for the deviations to cancel out was found when considering the algebraic means of the deviations. Over a long series, monthly counts will thus give a rather accurate picture of the population levels even if some months show deviating values (cf. Matthews 1960, Nilsson 1967 a). It may also be mentioned that only slight differences were found between annual indices calculated from monthly counts and counts twice a month.

Calculations of the coefficient of variation (V), i.e. the standard deviation as per cent of the mean of the counts showed the variation to be fairly high (Table 2, cf. also Matthews 1960). It may be noted that for the Goldeneye, V was considerably higher in the Öresund than on the south coast.

The calculation of annual indices from the counts

The "midwinter counts" made in Scania in 1964-70 can be used directly to study the changes in the midwinter populations of diving ducks on the coasts of Scania in those sectors that were counted every year. However the full data can be used by comparing the numbers on all localities counted in two consecutive years and calculating a primary index, i.e. the total of year B as per cent of the total in year A for those localities counted in both years. These primary indices are then recalculated in relation to the base-year =100. Indices were also calculated for those localities counted every year expressing the totals as per cent of the total in the base year (1966/67). The two sets of indices did not show any significant differences so the indices based on comparisons between paired years will be used as they are based on larger material.

The single "midwinter count" will be affected by too many factors, e.g. bad weather conditions, shorter cold periods near the count date, changing ice conditions etc., to give an adequate picture of the annual fluctuations in the wintering duck populations. The situation is different in

the International Midwinter Counts, where most parts of Europe are covered simultaneously and where the ducks driven away from one area by ice will be counted in another area.

In a restricted area such as Scania repeated counts will give a better basis for studying the annual changes in the wintering and resting populations especially when the counts are made in the same manner by the same observer on all occasions. The counts in the two coastal study areas were thus used to calculate annual indices (Fig. 14). The totals from all mid-monthly counts in September-April were expressed as per cent of the total in 1966/67. In 1962/63 and 1963/64 counts were only made in Lommabukten and the indices for these two seasons were obtained similarly as per cent of the total for Lommabukten in 1966/67.

Another set of indices were calculated for Lommabukten 1962/63-1967/68 and the south coast 1964/65-1967/68 using counts twice a month. Comparison between the indices based on counts twice a month and once a month did not show any significant differences except for the Scaup in two years but the tendency here was the same. No significant differences were found when the two study areas were compared except for the Tufted Duck in 1965/66, when local ice conditions probably influenced the results. It is thus justified to use one index for both study areas based on monthly counts.

An index calculated in this way from monthly counts will measure both the population level and the period the different species stay in the area, thus the use the populations make of a certain area. If the period of stay does not show any consistent trend but only variations according to the weather situation in the different years a series of indices from different years will be a good indication to the changes in the population. It will also be a better measure than single counts as it considers the whole period of importance for the different species. When comparing two years it must however be remembered that the indices are influenced not only by population level but also by the period of stay.

Indices based on monthly counts were used in studies of the annual changes in duck populations in Britain (Atkinson-Willes & Frith 1965, Eltringham & Atkinson-Willes 1961) and at the Lake of Constance (Sziij 1963).

5. Seasonal appearance in Scania of the species investigated

Movements from inland Sweden to the coasts of Scania

The wildfowl counts in Sweden that started in 1959 provide a means of following the movements of the duck populations from one region of southern Sweden to another. Counts were made at a number of localities dispersed over the country from Scania to the provinces of Värmland and Uppland from September to April or May. The organization of the counts and the localization of the counting localities have been described by Nilsson (1968 a).

In all species of diving ducks a good correlation was found between the decrease in numbers on inland waters and the increase in numbers on the coastal waters in Scania (Fig. 3). Some differences were found between the different species. The Tufted Duck reached peak numbers at the coasts of Scania in midwinter, whereas Tufted Ducks only occurred in large numbers on the inland waters in autumn and spring. In the Pochard, Aythya ferina (L.), a decrease was found on both inland and coastal waters during the autumn but some Pochards remained on the coastal waters during the winter. In both the Goldeneye and Goosander, peak numbers at the coastal waters occurred during the winter after an autumnal peak on inland waters in November. All species showed a marked inland migration in March or April.

Fluctuations in the duck populations in Scania during the winter

The seasonal pattern of appearance in the three study areas in 1964/65-1967/68 was different for the different species showing rather marked fluctuations (Figs. 5-13). Similar results were obtained in the other years with less frequent counts. This variation was most marked in periods with partial ice cover. In the two coastal areas the numbers counted during November-March were well correlated with the mean temperature for the week preceding the count (as measured at Malmö) (Table 3) with the highest numbers during the coldest periods. In 1964/65 no such correlations were found in the Öresund area as the area was covered with drifting ice for a period. The same was the case for both areas in 1965/66.

The Scaup (Fig. 5) was only found in any numbers in the Öresund area. The autumn migration occurred in November-December followed by fluctuating numbers during the winter and a peak in March with appreciable numbers staying in April. The main arrival in spring was simultaneous with the onset of milder weather. On the German coast of the Baltic the Scaup was commoner in March than in January in Mecklenburg (Nehls 1963, 1967, 1968 a,

1969) whereas the situation was the opposite in Schleswig-Holstein (G.A.J. Schmidt in litt.). This might be taken as an indication that most Scaups pass on rather rapidly to the southwest in the autumn with only a few resting, whereas spring migration is slower with larger numbers resting on the way.

In the Tufted Duck (Fig. 6) the main increase at the coastal areas in Scania occurred in October/November, i.e. simultaneously with the decrease on the inland localities in south Sweden. In spring the decrease at the coasts and the inland migration was simultaneous with the onset of milder weather. During the winter the numbers fluctuated but most Tufted Ducks stayed even during hard ice periods so long as some open water was available. It may be noted that high numbers occurred on Lake Ringsjön in autumn when the other lakes only had a few Tufted Ducks.

The Pochard (Fig. 7) was only found in any numbers on the lakes and in the Öresund area, where maximum numbers were found simultaneously in the autumn. Numbers were low during the winter but in 1967 larger numbers than usual stayed until December. Spring migration was not marked.

The Goldeneye (Fig. 8) was common in all the three areas. The autumn peak occurred earlier in the lake area than at the coasts, where the main arrival was simultaneous in the two study areas. On the south coast a peak was reached in midwinter, whereas in the Öresund area there occurred a steady increase to a peak during spring migration. The spring migration was initiated earlier on the south coast than in the Öresund area, the latter probably being more favourable for the Goldeneyes and thus causing them to stay longer. The spring peak at the coasts was correlated with the first main increase in temperature and inland migration started as soon as the lakes became free of ice. In 1966 a second peak in April was related to exceptionally low temperatures.

The Long-tailed Duck (Fig. 9) was only counted in single individuals in the Öresund area but was common on the south coast, where it appeared in November-December showing an increase to a peak in late winter or early spring. In 1966 a marked delay with unusually high numbers counted was related to exceptional temperatures in April. In the same way the record for mid April 1970 was exceptionally high; 9,100, caused by delayed migration this late spring.

Eiders, Somateria mollissima (L.), were found in moderate numbers on both the south coast and in the Öresund (Fig. 10). The highest numbers were found during the migration in autumn and spring.

Red-breasted Mergansers, Mergus serrator L., (Fig. 11) were only found

in large numbers on the south coast, where they arrived in November and left in March-April. In 1966 a second peak occurred in April related to low temperatures.

The Goosander arrived in the lake area in November when the first few individuals were also seen at the coasts (Fig. 12). The main arrival at the coasts did not occur till the lakes were ice-covered and the Goosanders generally left the coasts as soon as the lakes were free of ice.

The Smew, Mergus albellus L., was counted in small numbers in the Öresund area and on the lakes from November-April (Fig. 13). In autumn it appeared in the same period both at the coast and the lakes, whereas a peak was noted on the lakes after most of the Smews had left the coast in spring.

6. The size of the wintering diving duck populations in Scania

The "midwinter counts" showed that the diving duck populations excluding the Long-tailed Duck, Velvet Scoter and Common Scoter that stay too far out at sea to be adequately counted varied between the minimum numbers of 19,200 and 35,700 in the different years with an appreciable proportion in the two study areas (Table 4). The actual numbers were somewhat higher as a small proportion of the coast was not counted each year. However all areas of any importance were counted every winter so probably less than 5 % of the diving ducks escaped counting by staying in these areas.

The lakes in Scania have been frozen at the "midwinter count" and open water has only been available at the coasts and on some rivers. Small numbers of Tufted Ducks, Goldeneyes, Goosanders and a few Smews have been counted here, but the totals were insignificant in relation to the numbers wintering on the sea, except for the Goosander and Smew during mild winters.

No counts are available from the offshore waters of Scania in the periods of the "midwinter count" but some boat censuses were made to delimit the distribution of different species. In January 1966 2,742 Long-tailed Ducks were counted from a boat off the south coast the day after the "midwinter count" whereas 485 were seen from the shore. In January 1967 the figures were 2,581 and 515 respectively. No boat censuses could be made on the east coast of Scania in January but in December 1966 7,870 Long-tailed Ducks were counted here. Similar values were obtained during other censuses. It is impossible to estimate the population of Long-tailed Ducks wintering off the coasts of Scania from the few counts made, but it was certainly well above 10,000. The number of Velvet Scoters was much smaller probably more than 500 and the Common Scoters were even more

sparse off the coasts of Scania in winter.

The International Midwinter Counts (cf. Nilsson 1968 b) have only been made for four years and it is thus not yet possible to estimate the size of the January population of the different species in Sweden with any certainty. In the Tufted Duck, however, the counts were rather complete. This species rosts in large flocks on traditional sites most of which were counted in January 1969 yielding a total of 60,200 individuals, 25,200 of which were counted in Scania that thus harboured an appreciable proportion of the Swedish winter population of this species. In the other more dispersed species the counts were less complete.

7. Annual changes in the diving duck populations on the coasts of Scania

Annual changes in the indices were found in all species in varying extent (Fig. 14, Table 5), some species showing wide fluctuations between the different years, other species showing significant trends.

In the Scaup the indices showed marked fluctuations. The lowest index was noted in 1962/63, when most parts of Lommabukten were frozen. The index was probably too low as the Scaups normally staying here probably stayed in another part of the study area not counted that year. No midwinter indices were calculated for this species as some of the "midwinter counts" were probably not fully representative for this species as some Scaups might have been missed among the more numerous Tufted Ducks.

In the Tufted Duck a marked upward trend from 1963/64 onwards was found in the indices both from the monthly counts in the study areas and the "midwinter counts". 1962/63 showed a deviating index, but it must be remembered that this winter was extremely cold and that only part of the areas was counted. In the normal winter 1963/64 the index for Lommabukten was more representative for the general situation in the study area. It may be noted that the regression coefficients for both indices were the same.

The Pochard occurred mainly in Lommabukten so the indices from 1962/63 and 1963/64 may be regarded as fully representative. The indices showed only fluctuations with a marked peak in 1964/65 related to a flock staying in the area longer than usual.

The Goldeneye showed wide fluctuations in the indices. Three peak years differed from the other years: 1962/63, 1965/66 and 1969/70, i.e. the ice-winters when larger numbers than usual congregated at the coasts of south-west Scania. The midwinter indices on the other hand showed a low index

for 1965/66 probably related to the ice situation in other parts of Scania. In 1969/70 most coastal areas in Scania were free of ice at the "midwinter count" whereas most areas further to the north were frozen and a high index was noted.

In the Long-tailed Duck a steady level was noted with the exception for 1969/70, when larger numbers than usual had assembled in the south coast study area. As was noted above the Long-tailed Ducks normally stay far out at sea and thus cannot be counted from land with any accuracy. In part of the south coast study area, the situation was different and the Long-tailed Ducks could be counted from the shore by telescope in good weather. The indices for this species were solely based on counts in this area, that harboured the majority of the Long-tailed Ducks in the study area.

The Eider indices showed an increase both in the study areas and in the midwinter indices. It must however be remembered that the Eider population in Scania during the winter season was very small.

The Red-breasted Merganser also showed an upward trend in the indices from the "midwinter counts", whereas the indices from the study areas only showed fluctuations.

The Goosander finally showed a marked increase in the indices over the whole period. The midwinter index for 1964 was markedly higher than the index for the study area due to the inclusion of an unusually large flock. The same was the case for 1970.

8. The composition of the wintering diving duck populations in Scania and neighbouring areas of the Baltic

The International Midwinter Counts that started in 1967 provide a means of studying the winter distribution of the diving ducks in the southern parts of the Baltic as almost complete counts were made in large areas of coastal waters (Joensen 1968, Nilsson 1968 b, Nehls 1963, 1967, 1968 a, 1968 b, 1969, G.A.J. Schmidt in litt.).

The "midwinter counts" from Scania in 1964-70 and the International Midwinter Counts in Sweden 1967-70 were used to calculate the mean composition of the diving duck populations on the inshore waters in three parts of Scania, in four Baltic areas north of Scania and in inland Sweden (Table 6). Some differences occurred between the different years but they were not significant. No counts were made at sea so the species staying far out, i.e. the Long-tailed Duck and the Scoters were under-represented and thus not included in this comparison. The counting localities used

in 1967 and 1968 can be seen on a map in Nilsson (1968 b). The counts in 1969 and 1970 also included almost the whole coast of Öland and Gotland and many other areas on the Baltic coast.

When comparing the composition of the diving duck populations of these districts marked differences are found. On the inland waters the Goosander and Goldeneye dominated markedly with some Tufted Ducks and the other species only occasionally seen. The proportion of Goosanders was much lower in all other areas whereas the Goldeneye had almost a high proportion of the population on the south coast of Scania.

The Tufted Duck was the dominating diving duck in all inshore areas in the Baltic and the Öresund. On the south coast of Scania it was however only slightly more common than the Goldeneye. The Goldeneye was also fairly common in the other areas with open coast, i.e. Scania, Gotland and Öland, whereas it was less frequent in the archipelago areas. Among the mergansers the Goosander was the clearly dominating species in all areas except Öland, where the Goosander and the Red-breasted Merganser were equally common. In all off-shore areas of the Baltic the Long-tailed Duck was the only really common species.

Comparing the counts from Sweden with the counts made on the Baltic coast of Germany (Table 6) it is seen that the diving duck population of the Mecklenburg coast was similar to that of the Baltic coast of Scania in having a high proportion of Tufted Ducks. Some differences were however found, e.g. Scaup and Pochard were more common here. In Schleswig-Holstein the proportion of Tufted Ducks was lower and the Eider was an important species. Moreover the Scaup was much more common here than in the other Baltic areas.

The wintering duck populations in Denmark were extensively surveyed from the air in November 1967 and January 1968 (Joensen 1968). On north and east Zealand the diving duck populations were similar to that of the Öresund on the Swedish side with a high share of Tufted Ducks. This species was also common on S. Zealand whereas the Eider was the dominating species in most other areas. The Scaup and Pochard were important in some localities but Goldeneyes were found in all districts, being a common species. Finally the Long-tailed Duck was only seen in numbers around Bornholm and off S. Zealand. Among the mergansers the Goosander dominated over the Red-breasted Merganser in all areas.

Thus the diving duck populations of the Baltic showed a change in the composition from the north and east to the south-west, i.e., the main direction of the autumn migration (cf. Boyd 1959, Nordström 1963, Harri-

son 1967). This picture will be obtained if the different species have different requirements in relation to temperature etc. and thus stopping in different regions with the most resistant species in the north near to the ice.

9. Conclusions

The different species of diving ducks have different diving abilities and with the formation of ice the inferior divers will have difficulties in finding sufficient quantities of food in the northernmost areas. This might result in the marked regional differences in the composition of the diving duck populations discussed in § 8. The dominance of an excellent diver such as the Long-tailed Duck in offshore areas of the Baltic may be seen in relation to this factor. Other aspects of the feeding ecology will also be of importance. The Tufted Duck and the Goldeneye can dive to almost the same depths but the Tufted Ducks normally feed only at night but both at night and day during hard periods whereas the Goldeneye is restricted to daytime feeding. In midwinter the Tufted Ducks thus have a much longer time for feeding than the Goldeneye and thus the dominance of Tufted Ducks over Goldeneyes was more marked in the northern parts of the Baltic and especially in the archipelago areas than in areas further to the southwest. Goldeneyes were also found to leave the study areas to a larger proportion during cold ice periods than the Tufted Ducks that mostly stayed as long as open water was available.

The winter distribution of the different species will also be influenced by factors other than the possibilities in finding sufficient food supplies, although the food factor is probably the ultimate factor underlying the differences in winter distribution (cf. Lack 1968). Tradition might be a factor of importance in the regional distribution as well as in the local distribution. Moreover the reaction of the birds to the geography of the region might be of importance in relation to the migration patterns of the different species. The Long-tailed Ducks follow the Baltic coast on the migration and thus do not enter the Öresund, while the commonest species in this area, Tufted Duck and Goldeneye, are also common inland during migration and will probably reach the Öresund area after an inland migration.

When discussing Scania as a winter-quarter for diving ducks it must be noted that Scania is a fringe area for many wintering duck populations (cf. Atkinson-Willes 1969). Most parts of the Baltic coast north of Scania, except Öland and Gotland, freeze every winter whereas the coasts

of Scania have an ice-cover only during the coldest periods and even then some open water is generally available.

The severity of the winter is thus a factor of importance for the duck populations along the coasts of Scania and the local distribution and the numbers of some species vary in relation to the severity of the winter, e.g. the Goosander was found in larger numbers in winters with much ice further to the north as was the Goldeneye.

In addition to the ice-conditions the temperature is also an important factor in timing the appearance of the diving ducks in Scania. A significant correlation was found between low temperatures and high numbers of most species. The increase in numbers at the coasts of Scania was well correlated with the departure from the inland waters in south Sweden as was the departure from the coast. The migration in spring was well correlated with the onset of milder weather.

In light of these relationships between the temperature and ice-situation and the numbers of wintering diving ducks in Scania marked variation in the annual indices could be expected. This was also found to be the case. The amplitude of the fluctuations in Scania was much greater than at the Lake of Constance, an important winter area for ducks further to the south (cf. Szijj 1963).

Trends were found in the populations of some species: Tufted Duck, Eider, Red-breasted Merganser (midwinter) and Goosander. The winter-populations of Eider and Red-breasted Merganser in Scania are very small and the observed trends are probably only of local character. In the Tufted Duck on the other hand the upward trend was noted for a population that makes up a significant proportion of the Swedish winter population. It may be noted that a similar trend was found on wildfowl count localities in inland Sweden (Nilsson unpubl.). Similarly, the upward trend in the Goosander was paralleled on the wildfowl count localities.

Comparable data from the wildfowl counts in other countries have not been published except for Great Britain (Harrison 1967). The Tufted Duck showed a marked increase up to 1957/58 but has then fluctuated on a steady level (Harrison op.cit., Atkinson-Wilkes in litt.). For the other species there are no published indices. A discussion on the significance of the observed trends must thus await further counts in Sweden and especially the analysis and publication of the wildfowl counts in other countries.

Finally when considering the importance of Scania as a winter area for diving ducks the winter population here was found to be between 19,000

and 36,000 for the inshore waters excluding the Long-tailed Ducks and the Scoters. This means that Scania is the most important winter area for diving ducks (excluding Long-tailed Duck and the Scoters) in Sweden, only Gotland having at all comparable numbers of wintering diving ducks (Högström 1965, Nilsson 1968 b, Wiss 1965). Compared with other winter areas, e.g. the Netherlands, parts of Denmark and the Baltic coast of Germany, Scania is however less important, being situated on the northern fringe of the winter-distribution of many diving ducks (cf. Atkinson-Willes 1969).

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I wish to express my sincere thanks to Professor P. Brinck, Head of the Department, for working facilities and valuable advice. My sincere thanks are also due to Dr. S. Ulfstrand for valuable advice and criticism. I am also much indebted to Mr. H.W. Nohls and Dr. G.A.J. Schmidt for providing unpublished data from Germany and to Mr. G. Atkinson-Willes for information on British Wildfowl Count data. Finally I wish to thank all those who have participated in the "midwinter counts".

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Table 1. Mean change in numbers of diving ducks between a count on day 0 and a count on day 0 + X. n = number of comparisons.

Species	Area	X=1-5		n	X=6-10		n
		Mean change (%)	arithm. algebr.		Mean change (%)	arithm. algebr.	
<i>Aythya marila</i>	Öresund	26	+6	15	38	-3	45
<i>Aythya fuligula</i>	Öresund	23	+2	20	41	+1	60
<i>Aythya fuligula</i>	South coast	29	+19	7	41	+2	13
<i>Bucephala clangula</i>	Öresund	32	+3	20	40	-3	56
<i>Bucephala clangula</i>	South coast	22	-9	7	23	-14	17
<i>Clangula hyemalis</i>	South coast	40	+1	6	59	+12	10
<i>Mergus serrator</i>	South coast	43	+42	6	41	+12	12
<i>Morgus merganser</i>	Öresund	35	-9	15	45	-30	23
<i>Mergus merganser</i>	South coast	39	0	7	35	-13	11

Table 2. Comparison between the monthly counts of diving ducks and mean values calculated from repeated counts in the same months. Mean coefficients of variation (V) within months are also shown. Months with more than three counts were used in the calculations.

Species	Number of		Mean deviation (%) of month-		Mean coeffi-
	months	counts	ly counts from average for month	algebraic	cients of Variation(V) within months
			arithmetic		
<u>Lommabukten</u>					
<i>Aythya marila</i>	12	50	24	+4	42
<i>Aythya fuligula</i>	22	84	25	+7	45
<i>Aythya ferina</i>	5	17	25	-8	37
<i>Bucephala clangula</i>	22	84	26	+7	51
<i>Mergus merganser</i>	5	24	16	+5	50
<u>South coast</u>					
<i>Aythya fuligula</i>	9	31	39	-5	40
<i>Bucephala clangula</i>	9	31	9	+5	24
<i>Clangula hyemalis</i>	5	17	26	-14	38
<i>Mergus serrator</i>	9	31	28	+12	46
<i>Mergus merganser</i>	7	25	30	+7	55

Table 3. Correlation coefficients for the relation between the number of diving ducks counted in the two study areas in November-March 1964/65 and 1966/67 and the mean temperature at Malmö for the week preceding the count. ^x, ^{xx}, and ^{xxx} indicate correlations significant for $P \leq 0.05$, $P < 0.01$ and $P < 0.001$, respectively. Number of counts in brackets in the head.

Species	1964/65		1966/67	
	South coast (12)	Lommabukten (19)	South coast (12)	Lommabukten (12)
<i>Aythya marila</i>	-	-0.26	-	-0.65 ^{xx}
<i>Aythya fuligula</i>	-0.79 ^{xxx}	-0.21	-0.73 ^{xx}	-0.35
<i>Bucephala clangula</i>	-0.66 ^x	-0.19	-0.75 ^{xx}	-0.58 ^x
<i>Clangula hyemalis</i>	-0.85 ^{xxx}	-	+0.32	-
<i>Mergus serrator</i>	-0.37	-	+0.09	-
<i>Mergus merganser</i>	-0.89 ^{xxx}	-0.17	-0.63 ^x	-0.83 ^{xxx}

Table 4. Total numbers of diving ducks counted along the coasts of Scania at the "midwinter counts" in 1964-1970.

Species	1964	1965	1966	1967	1968	1969	1970	Mean per cent of total counted in the two study areas
<i>Aythya marila</i>	1256	148	210	82	137	101	428	29
<i>Aythya fuligula</i>	9970	15178	10752	14425	21889	25058	18395	57
<i>Aythya ferina</i>	128	1	23	62	15	53	54	27
<i>Bucephala clangula</i>	6220	4552	5602	6237	3911	8119	8793	51
<i>Clangula hyemalis</i>	1053	4553	1535	2140	?	2456	?	30
<i>Melanitta fusca</i>	182	62	126	129	150	71	11	4
<i>Melanitta nigra</i>	53	126	33	1	161	6	24	2
<i>Somateria mollissima</i>	387	368	673	655	686	621	526	12
<i>Mergus serrator</i>	90	247	221	398	261	409	258	30
<i>Mergus merganser</i>	1147	554	1032	834	1180	1323	2852	40
<i>Mergus albellus</i>	25	45	10	37	33	67	54	59

Table 5. Statistical data to Fig. 14.

Species	Type of counts	Period	Correlation coefficient (r)	Probability (P)	Regression coefficient (b)
<i>Aythya marila</i>	Monthly	62/63-69/70	-0.04	$P > 0.9$	-
<i>Aythya fuligula</i>	Monthly	62/63-69/70	0.60	$0.2 > P > 0.1$	-
	Monthly	64/65-69/70	0.85	$0.05 > P > 0.02$	13.6
	Midw.	64-70	0.77	$0.05 > P > 0.02$	13.5
<i>Aythya ferina</i>	Monthly	62/63-69/70	0.22	$0.7 > P > 0.6$	-
<i>Bucephala clangula</i>	Monthly	62/63-69/70	0.56	$0.2 > P > 0.1$	-
	Monthly	64/65-69/70	0.76	$0.1 > P > 0.05$	-
	Midw.	64-70	0.57	$0.2 > P > 0.1$	-
<i>Clangula hyemalis</i>	Monthly	64/65-69/70	0.79	$0.1 > P > 0.05$	-
<i>Somateria mollissima</i>	Monthly	64/65-69/70	0.78	$0.01 > P > 0.001$	20.2
	Midw.	64-70	0.79	$0.05 > P > 0.02$	8.2
<i>Mergus serrator</i>	Monthly	64/65-69/70	0.60	$0.2 > P > 0.1$	-
	Midw.	64-70	0.77	$0.05 > P > 0.02$	13.1
<i>Mergus merganser</i>	Monthly	62/63-69/70	0.91	$0.01 > P > 0.001$	25.0
	Monthly	64/65-69/70	0.85	$0.05 > P > 0.02$	26.6
	Midw.	64-70	0.73	$0.1 > P > 0.05$	-
	Midw.	65-70	0.88	$0.05 > P > 0.02$	63.3

Table 6. Mean composition of the diving duck populations in inland Sweden and in different areas along the Baltic coast of Sweden and Germany and on the Swedish coast of the Öresund in January (Nehls 1963, 1967, 1968 a, 1968 b, 1969, Nilsson 1968 b and unpubl., G.A.J. Schmidt in litt.). As counts were made from the shore the Long-tailed Duck and Scoters that stay too far from the shore to be adequately counted are not included. Coastal areas unless stated.

Area	Ayth. maril.	Ayth. fulig.	Ayth. ferin.	Bucep. clang.	Som. moll.	Merg. sorr.	Merg. merg.	Merg. albell.
Sweden inland	+	12	1	45	-	+	40	2
Södermanland+Uppland	+	80	-	6	+	+	14	+
Gotland	7	72	+	14	1	3	3	+
Öland	1	50	-	28	2	9	10	+
Blekinge	+	88	+	5	+	+	6	1
Scania: East coast	2	67	1	19	4	2	5	+
South coast	1	47	+	43	1	2	6	+
Öresund	2	73	+	19	1	+	5	+
Mecklenburg	7 ¹⁾	43 ¹⁾	3	16	3	1	4	+
Schleswig-Holstein	22	36	1	14	24	1	3	+

1) 23 % *Aythya marila/fuligula*



Fig.1. Map of southwest Scania showing the general position of the study areas. The lakes of the lake study area are hatched on the map.

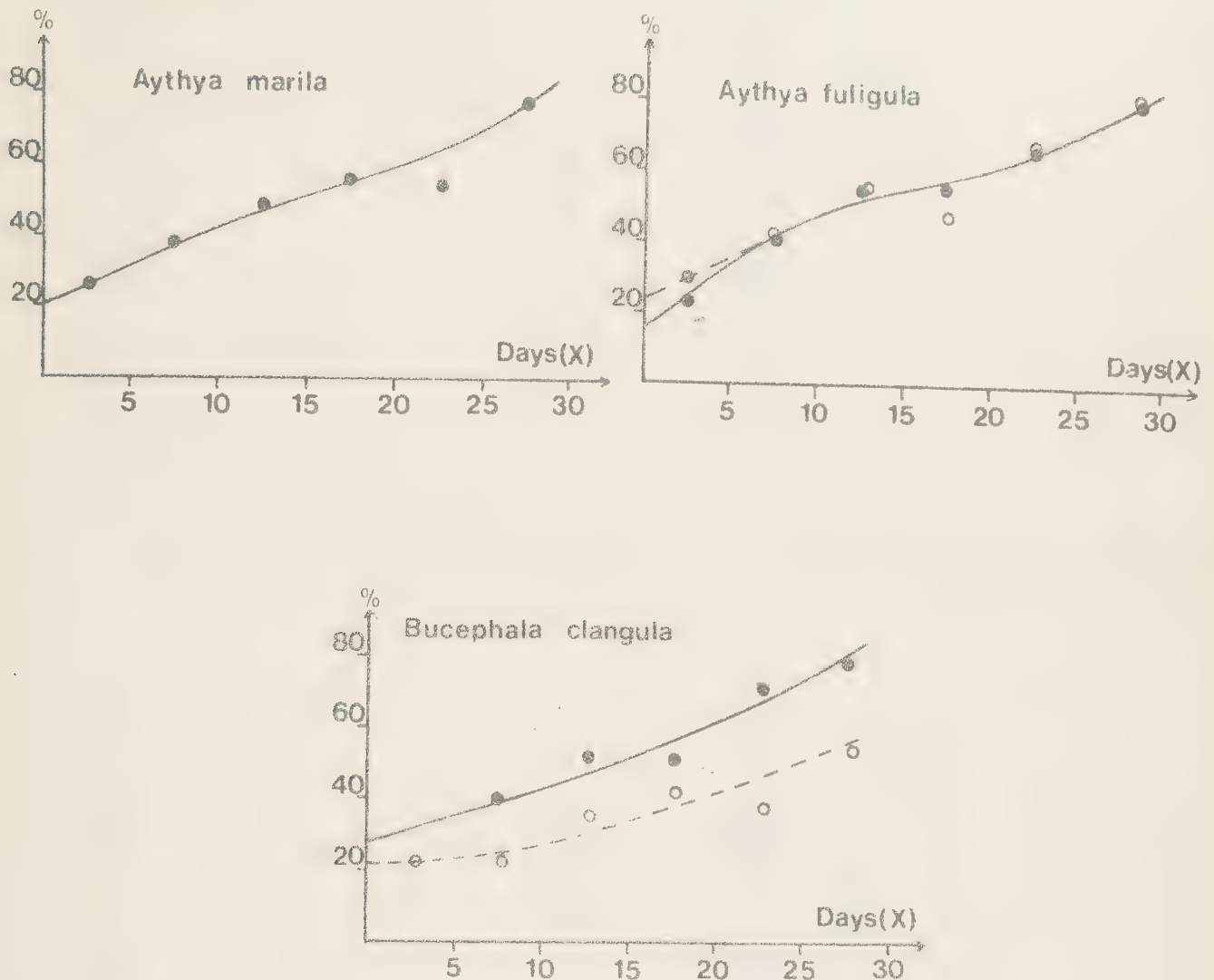


Fig.2. Mean change (in per cent) from day 0 to day 0+X in counts of Scaup, *Aythya marila*, in Lommabukten (218 comparisions), Tufted Duck, *Aythya fuligula*, in Lommabukten (311 comparisions) and on the south coast (104 comparisions) and Goldeneye, *Bucephala clangula*, in Lommabukten (279 comparisions) and on the south coast (118 comparisions). Open symbols and broken lines = south coast, filled symbols and whole lines = Lommabukten.

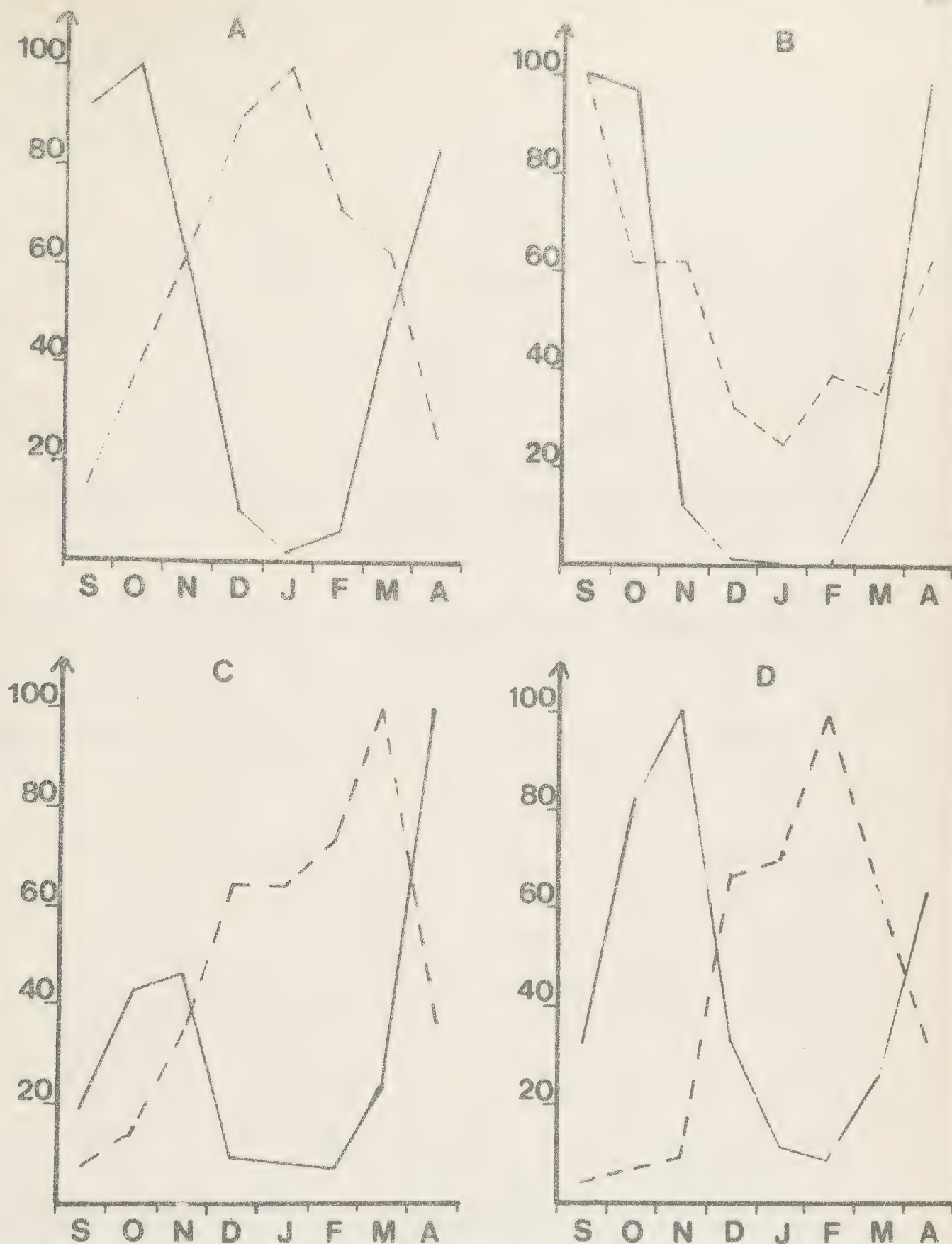


Fig. 3. Seasonal changes in Tufted Duck, *Aythya fuligula*, (A), Pochard, *Aythya ferina*, (B), Goldeneye, *Bucephala clangula*, (C) and Goosander, *Mergus merganser*, (D) on inland waters of south Sweden (—) and at the coasts of Scania (---) according to the wildfowl counts in Sweden in 1961/62-1968/69. For each year the counts in individual months were expressed as per cent of the maximum counts for inland and coastal waters respectively. The means of these percentages were then recalculated in relation to the highest mean = 100.

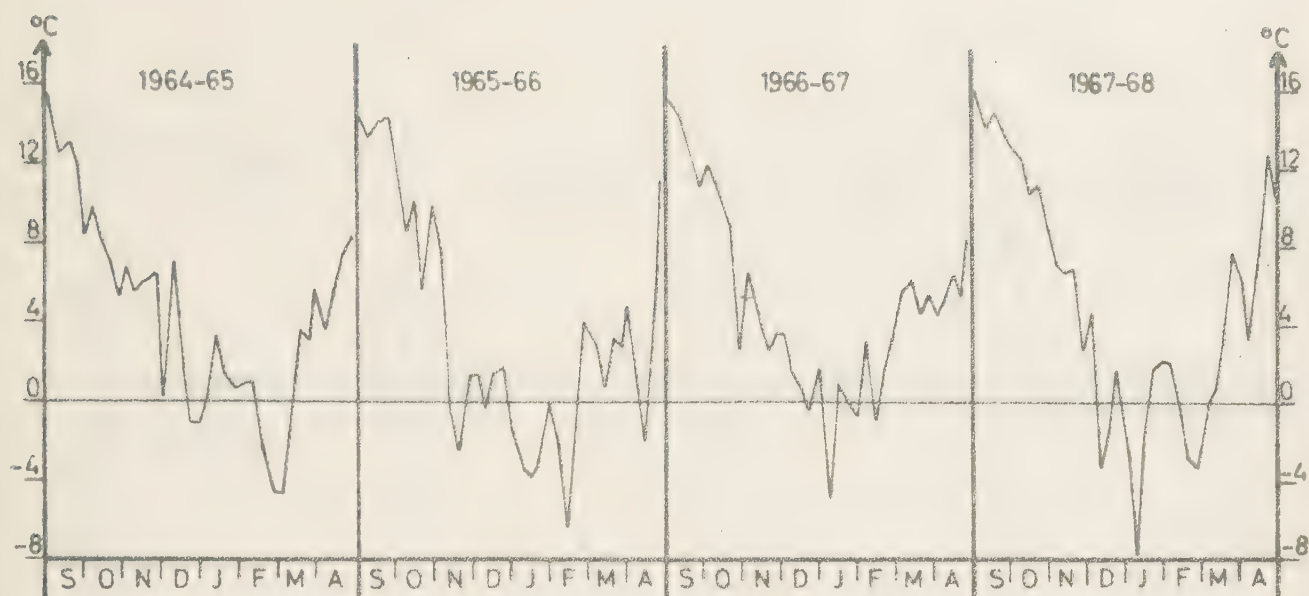


Fig.4. Weekly mean temperatures at 07.00 at Malmö 1964/65-1967/68.

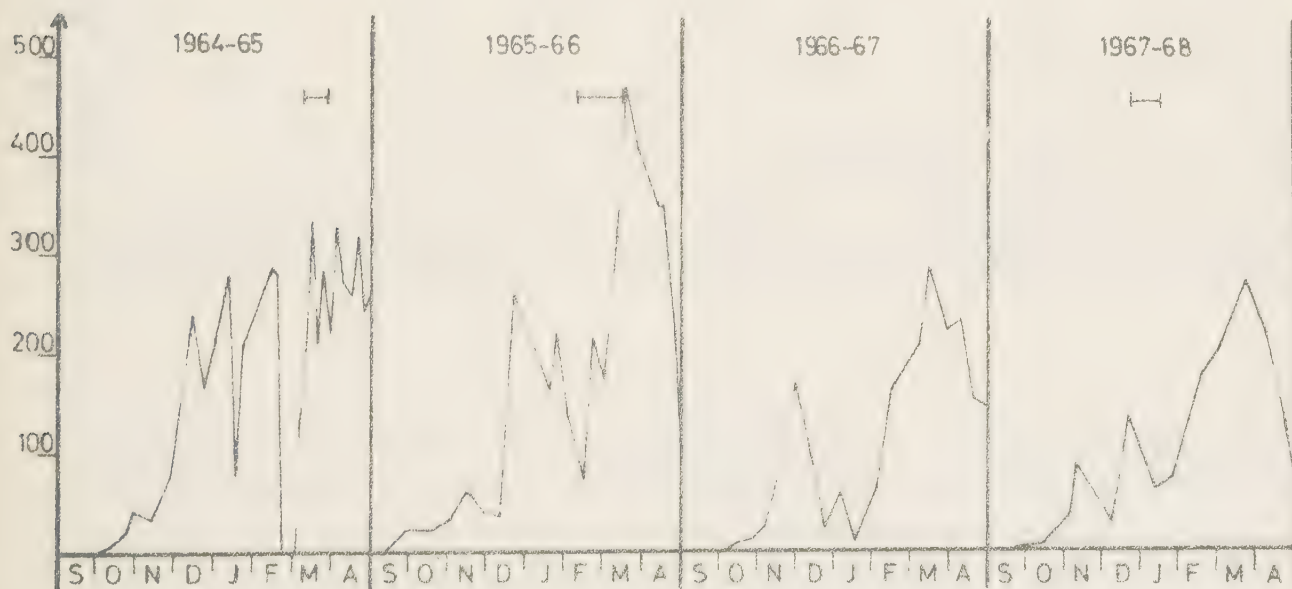


Fig.5. Counts of Scaup, *Aythya marila*, in Lommabukten 1964/65-1967/68.
Horizontal lines in the diagram show the ice-periods in the study area.

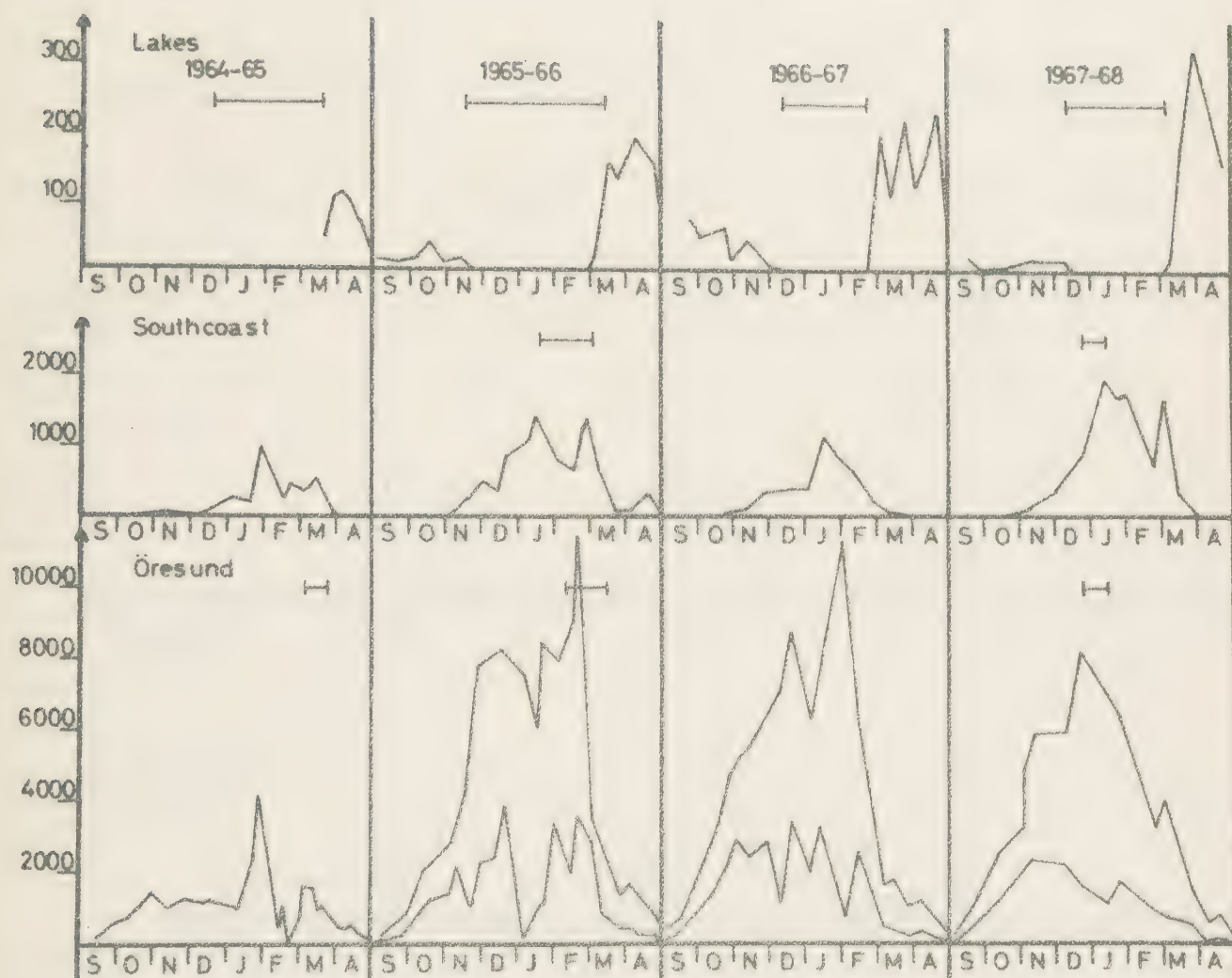


Fig.6. Counts of Tufted Duck, *Aythya fuligula*, in the three study areas in 1964/65-1967/68. In 1964/65 of the Öresund area only Lommabukten was completely counted so the curve for this year represents numbers counted here. In the other years the whole Öresund area was counted (upper curve in lower diagram) but the counts from Lommabukten are also shown (lower curve). Horizontal lines in the diagrams show the ice-periods in the study areas.

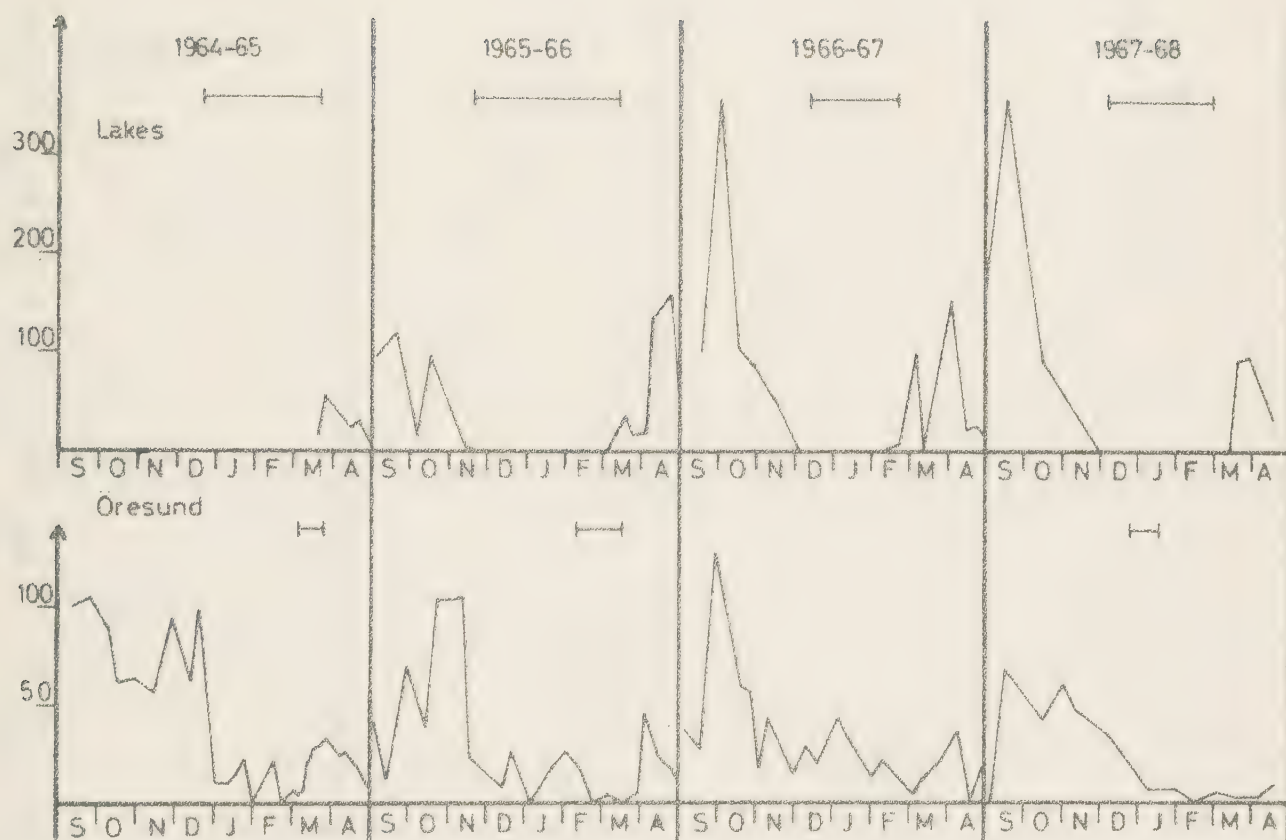


Fig.7. Counts of Pochard, *Aythya ferina*, in the lake area and in the Öresund area in 1964/65 - 1967/68. Horizontal lines in the diagrams show the ice-periods in the study areas.

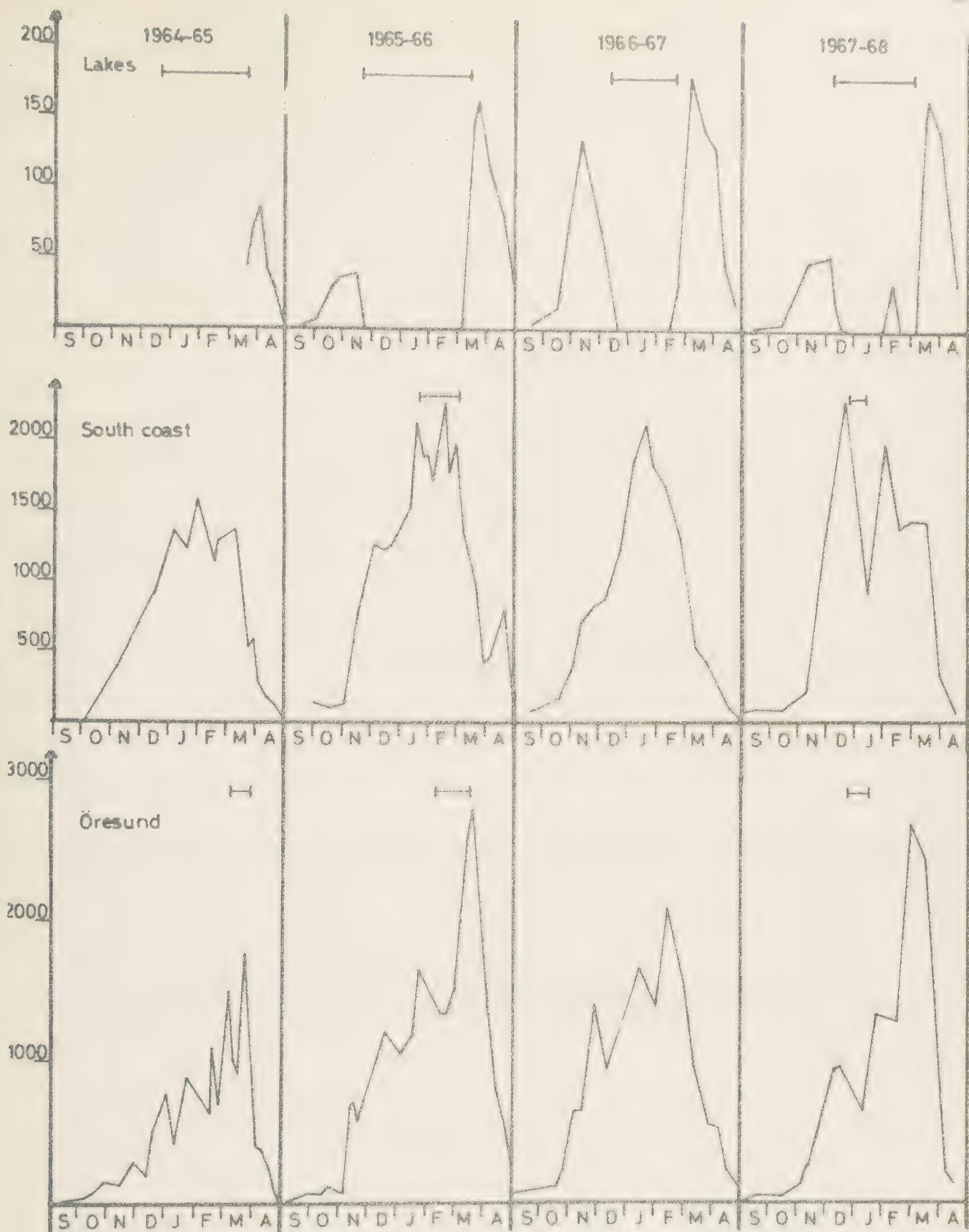


Fig.8. Counts of Goldeneye, *Bucephala clangula*, in the three study areas in 1964/65 - 1967/68. Horizontal lines in the diagrams show the ice-periods in the study areas.

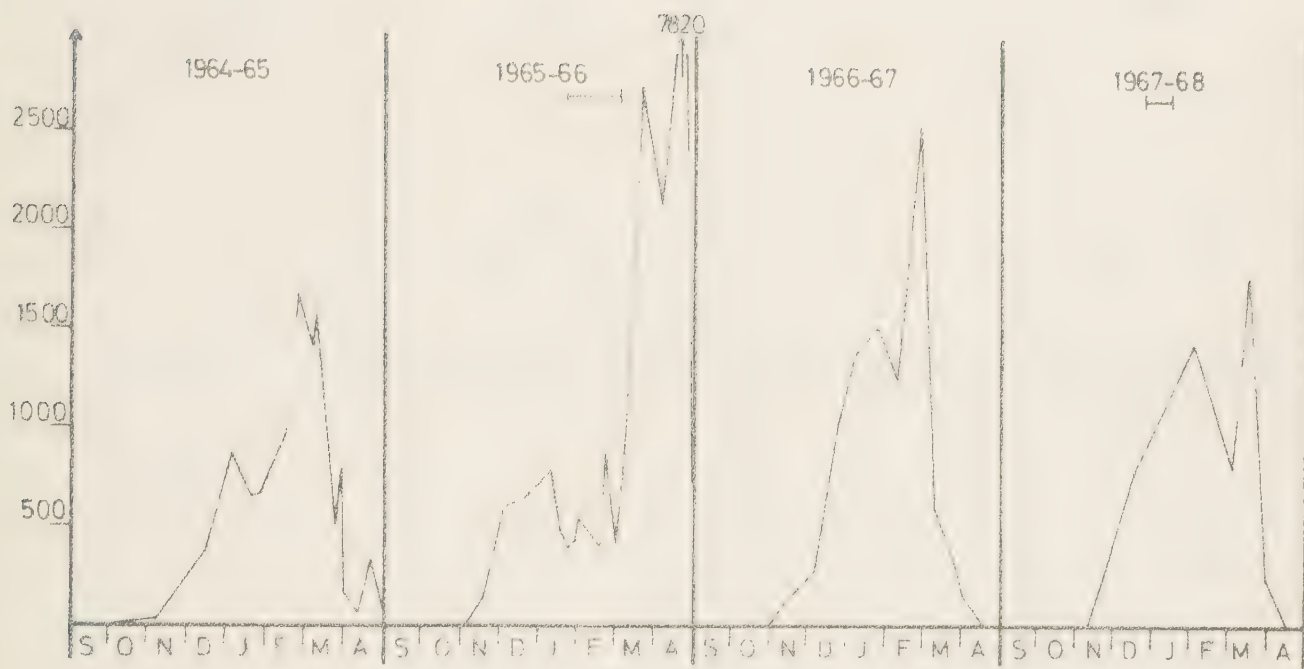


Fig.9. Counts of Long-tailed Duck, *Clangula hyemalis*, on the south coast in 1964/65-1967/68. Horizontal lines in the diagram show the ice-periods in the study area.

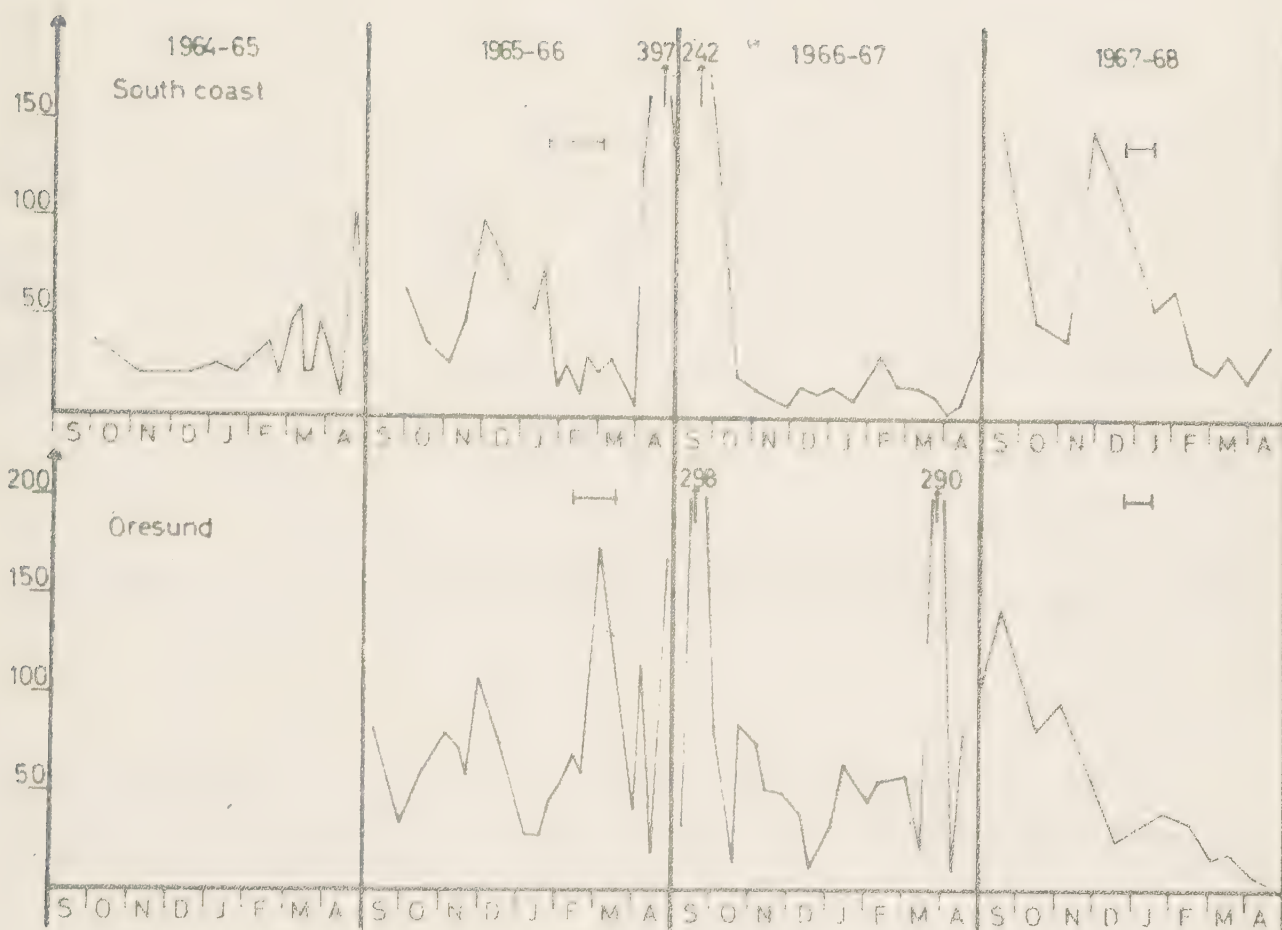


Fig.10. Counts of Eider, *Somateria mollissima*, on the south coast and in the Öresund area in 1964/65- 1967/68. Horizontal lines in the diagrams show the ice-periods in the study areas.

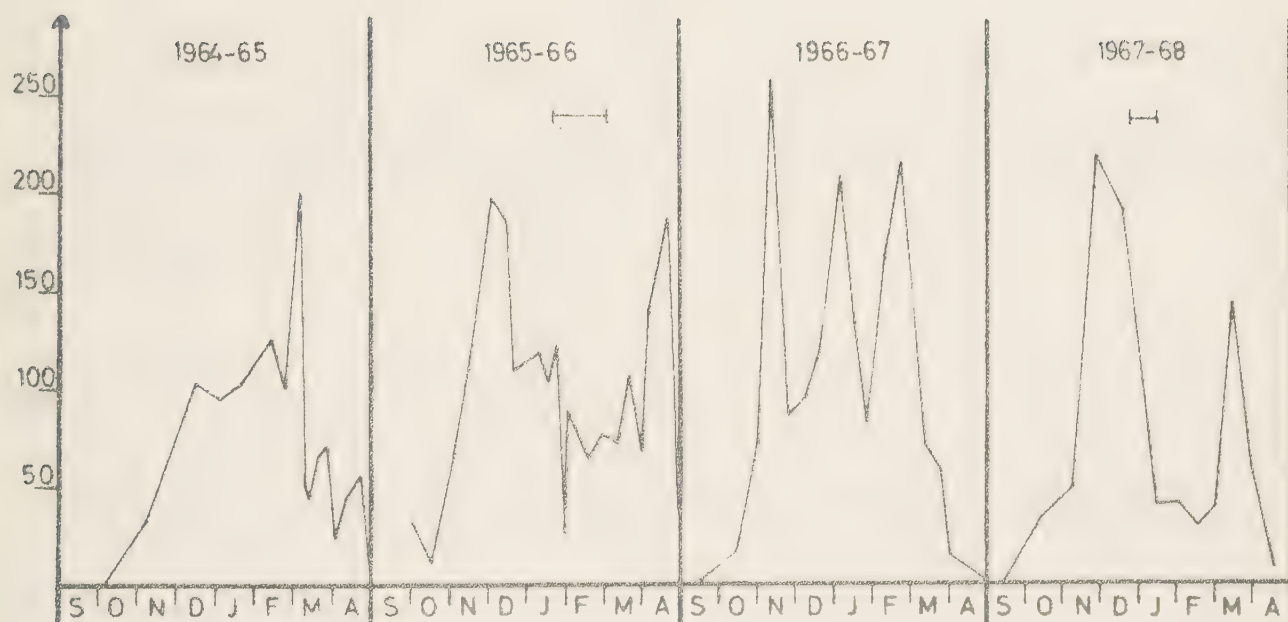


Fig.11. Counts of Red-breasted Merganser, Mergus serrator, on the south coast in 1964/65 -1967/68. Horizontal lines in the diagram show the ice-periods in the study area.

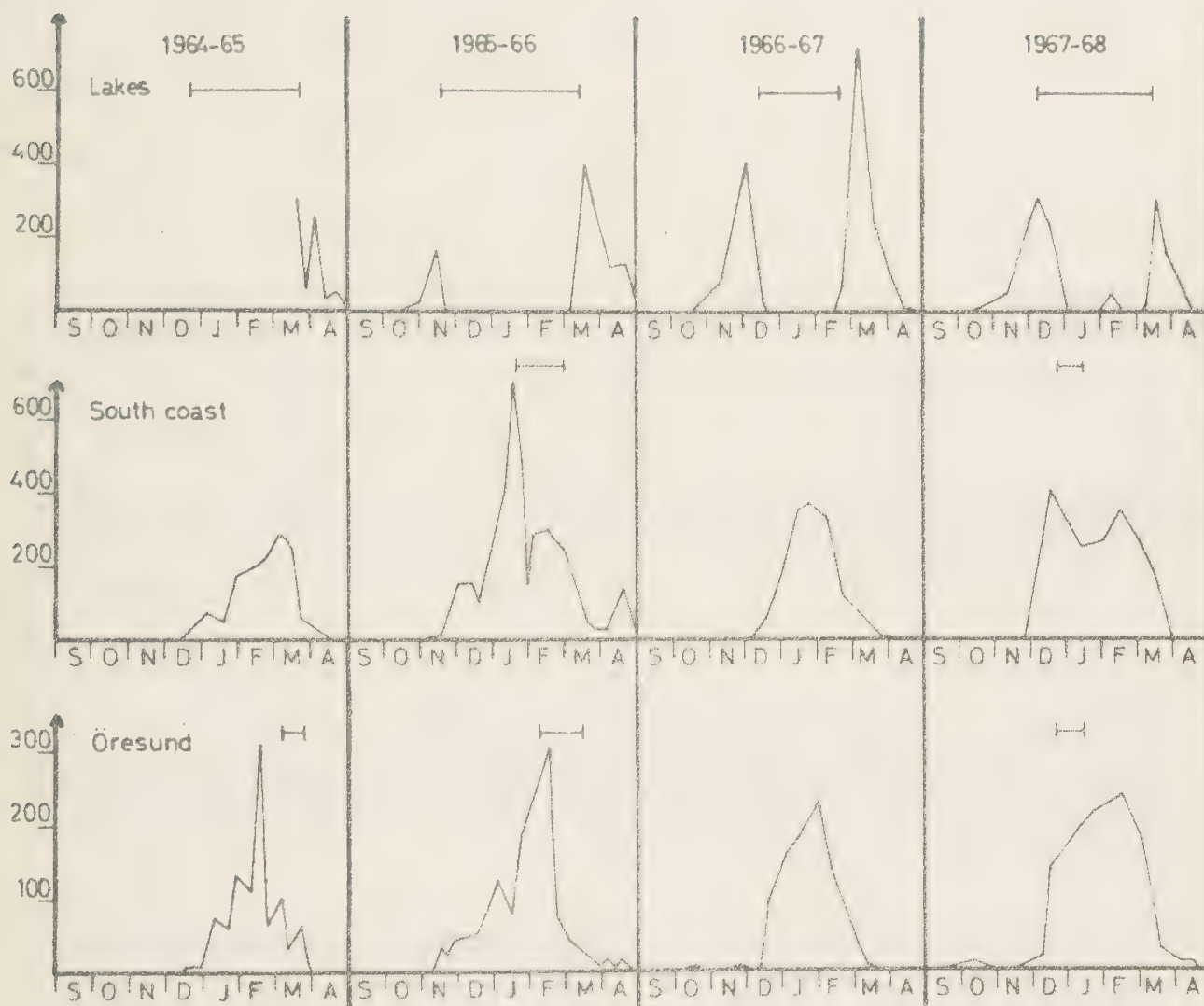


Fig.12. Counts of Goosander, *Mergus merganser*, in the three study areas in 1964/65-1967/68. Horizontal lines in the diagrams show the ice-periods in the study areas.

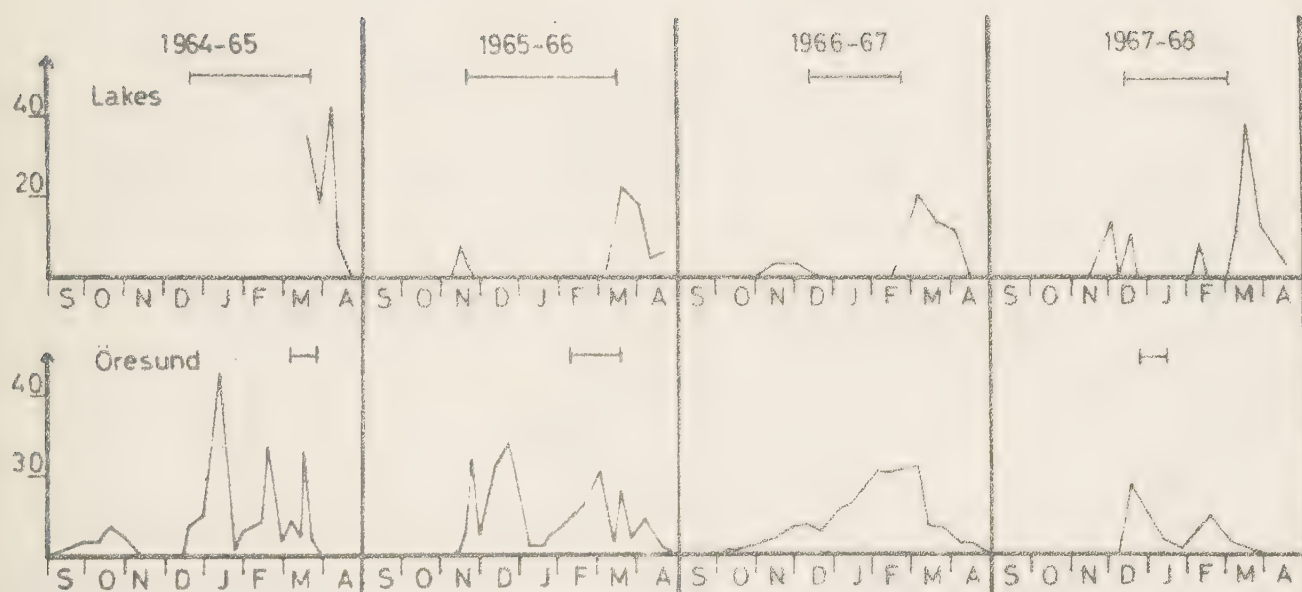


Fig.13. Counts of Smew, Mergus albellus, in the lake area and in the Öresund in 1964/65-1967/68. Horizontal lines in the diagrams show the ice-periods in the study areas.

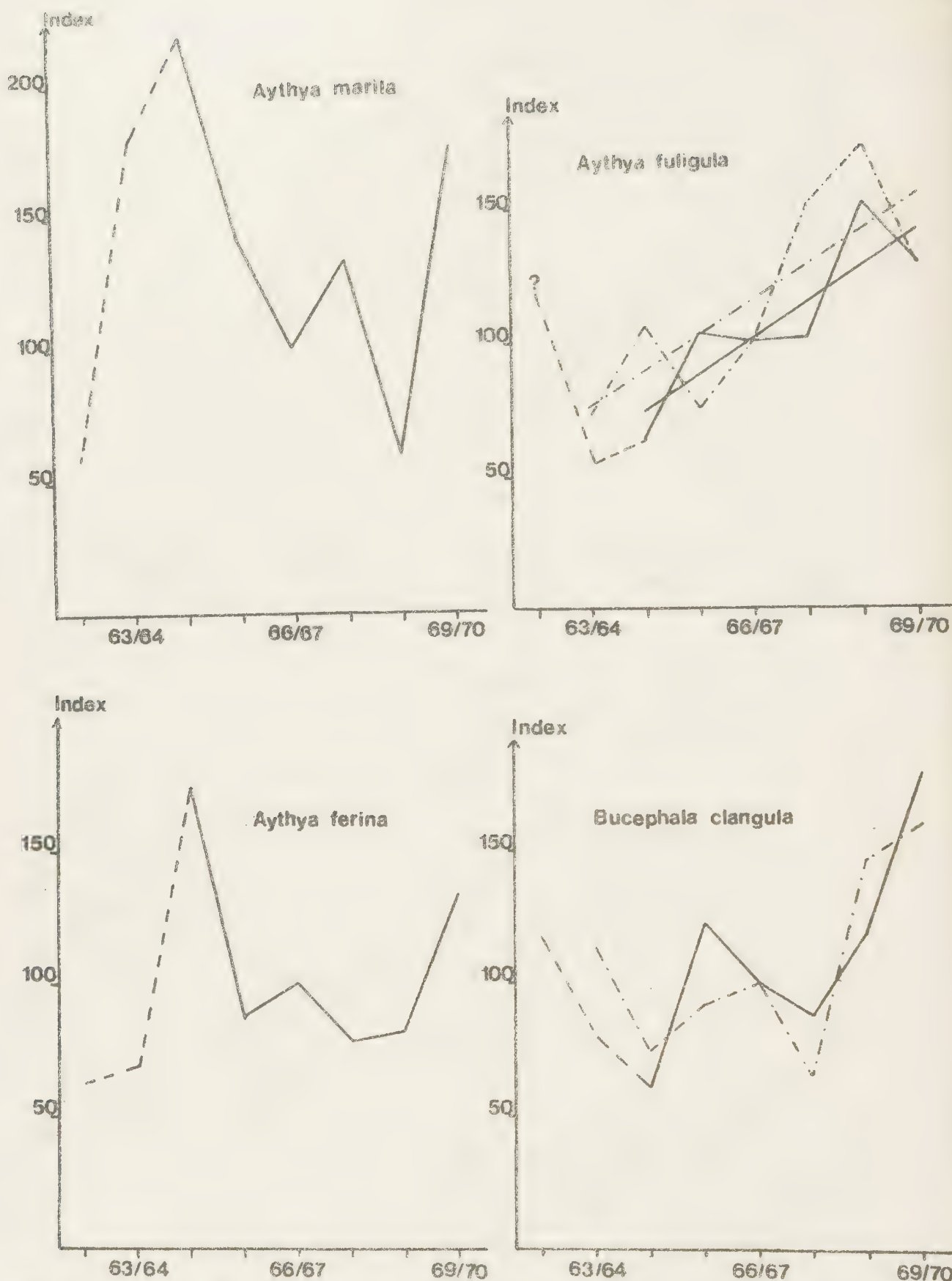


Fig.14. Annual fluctuations of the different species of diving ducks in Scania 1962/63-1969/70 from the monthly counts in the coastal study areas (--- and —) and the "midwinter counts (-.-.-). Broken lines connect values from the first two years when only Lommabukten was counted. Straight lines are regression lines. Statistical data are found in Table 5.

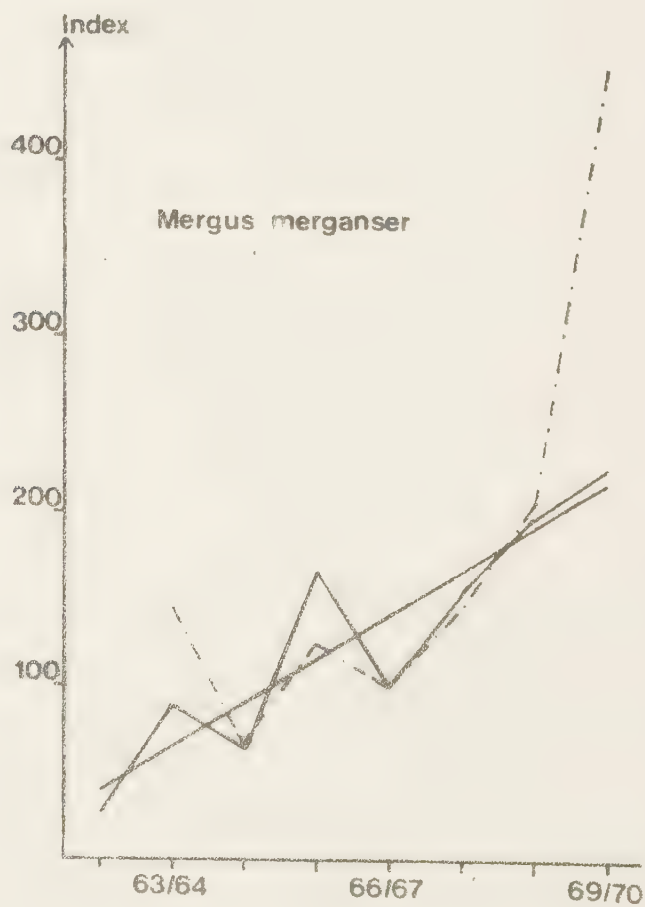
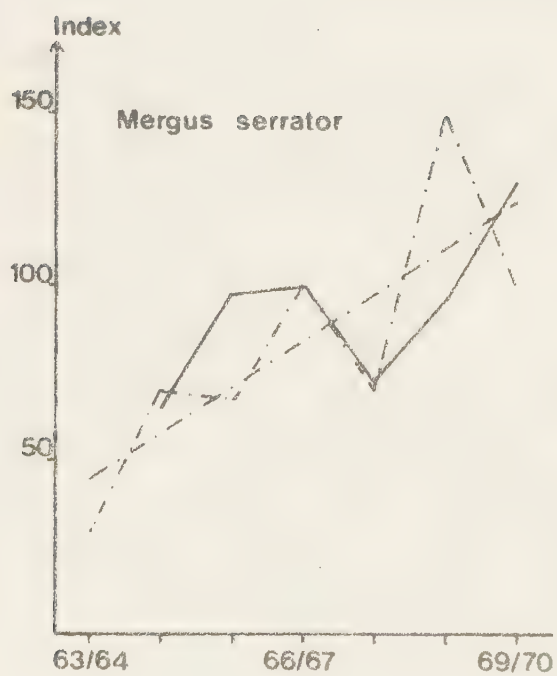
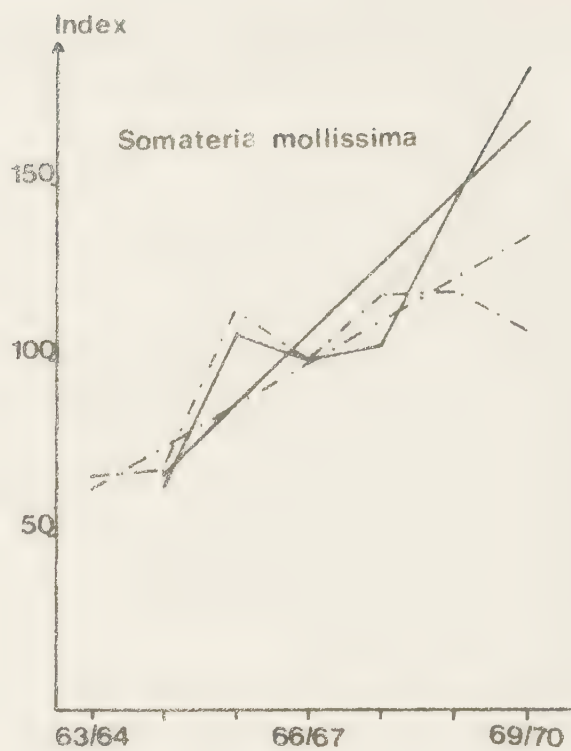
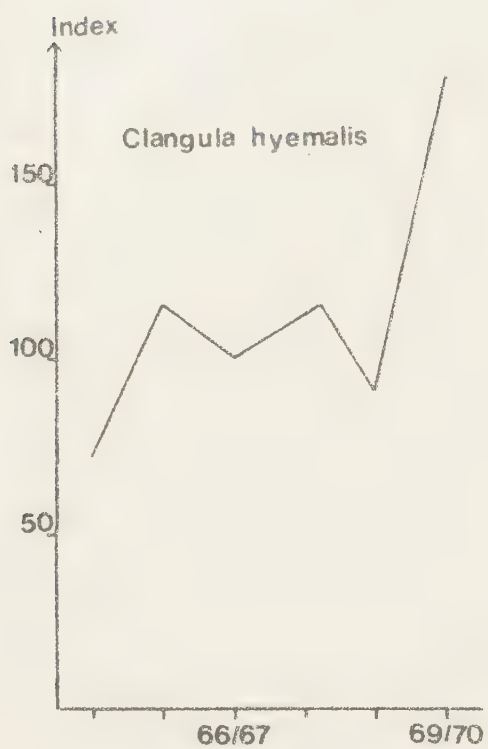


Fig.14. continued

Habitat selection, food choice and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season

ABSTRACT

The diving ducks wintering on the coasts of Scania showed an uneven distribution that was only partly caused by differences in the abundance of food and the availability of suitable resting places, tradition apparently being important. Differences in diving ability between the species were reflected in the local distribution. The Melanitta species occurred well offshore, Clangula hyemalis was mainly found offshore but also near the shore. Bucephala clangula mainly fed on shallow water near the shore and spent the night on traditional resting places some distance from the shore. The Aythya species spent the day on traditional resting places and fed at night, A. marila probably in deeper water than A. fuligula. Similarly in Mergus, M. serrator occurred offshore, M. merganser near the shore and M. albellus only in enclosed areas and river mouths.

The main food of the bottom-diving species was Mytilus edulis but the different species also took different additional food items. Macoma baltica was taken by A. marila and the Melanitta species, Hydrobiidae spp. and Cardium lamarekii were important for A. fuligula in some areas. B. clangula and C. hyemalis in addition to molluscs also took quantities of crustaceans and polychaetes.

The calculated rates of exploitation in different parts of the study areas showed that the food resources were sufficient for much larger numbers of ducks than present.

1. Introduction

The diving duck populations wintering in western Europe have been intensively studied during the last ten to fifteen years under the scheme of the International Wildfowl Counts with the aim of elucidating, among other things, the movements and annual fluctuations in numbers of the various populations (cf. e.g. Atkinson-Willes 1963, 1969, Nilsson 1968, Requate 1954, Szijj 1963), other aspects of the non-breeding ecology of most species have been little studied. Only one other extensive paper analysing the habitat selection of European ducks in the non-breeding season has been published (Szijj 1965) and rather few on the food of the diving ducks (cf. e.g. Cottam 1939, Madsen 1954). These papers did not discuss the relationship between the food intake of the ducks and the



food resources of their habitats which was, however, treated by Geramiscova & Baranova (1960) and Nilsson (1969 a).

The purpose of the present investigation being a part of a general study of the non-breeding ecology of diving ducks in south Sweden was to define the local distribution of the diving ducks in coastal waters and to analyse it in terms of food choice, feeding habits and the available food resources in different areas. The field work was performed during the winters 1964/65-1966/67 and 1969/70.

2. Description of the study areas

Observations were made in two study areas at the coasts of southwest Scania: Öresund from Saltviken to Klagshamn and on the south coast between Kämpinge and Ystad (Figs. 1-3) in 1964/65-1966/67 and at Sölvesborg in SV Blekinge (Fig. 1,4) in 1969/70. Complementary observations on the species staying far out at sea were made from the patrol vessels of the Swedish Coast Guard in the waters between Barsebäckshamn in the Öresund and Hanö in the Baltic (Fig. 14). The two study areas in SW Scania were divided into sectors (A-V and A-X, respectively) that will be referred to by letter in the text (Figs. 2 and 3).

Öresund study area

Most parts of this area are characterized by shallow water and soft bottom substrate (Fig. 2) with large areas only 1 m deep. The soft bottom made quantitative samples possible and the vast shallow areas at Bjärred (D-E) were accordingly selected for a more detailed study (Nilsson 1969 a). Quantitative samples were taken in all shallow areas and complemented with samples using a Birge-Ekman grab in the depth area out to 6 m. All bottom types were sampled both in autumn and spring.

Five natural bottom types were distinguished and a further type will be separated for the area around the Malmö harbour where the bottom has been markedly changed by building works. The species found on each bottom type are shown in Table 1.

1) Muddy bottom occurs mainly in the shallow areas (maximum depth 0.5-1 m) in sectors D, E, H and grades into the vegetation-free sand when going outwards from the shore except where it is separated from the sand by a belt of Zostera marina L. Some stones with Fucus vesiculosus (L.) and its associated fauna of Gammarus sp., Idothea baltica (Pallas) and I. viridis (Slabber) were found in parts of sector D. The vegetation on the mud consisted of low Zostera marina, Ruppia spp. and Zanichellia



palustris L..

The macro-fauna of the muddy bottom was dominated by Nereis diversicolor O.F. Müller, Hydrobiidae spp. and Cardium lamarekii Reeve.

2) Sand mixed with silt is represented in shallow water generally less than 0.5 m deep in sectors A, G, L, S and U where it grades into the vegetation-free sand in the outer parts or in sectors S and U into the Zostera-zone. In sectors A, G and H some parts were exposed at low water. Large stones with Fucus vesiculosus and its associated fauna were common in sectors S and U.

Vegetation was sparse and the macro-fauna was dominated by rather few species. Nereis diversicolor was found in large numbers in most areas and Cardium lamarekii was abundant especially in sectors S and U. Most species found on type 1 were also found on this bottom type but in smaller numbers.

3) Vegetation-free sand occurs as a narrow belt in sectors A, C-H separating the areas of bottom types 1 and 2 from the Zostera-zone. In sector D and parts of E the muddy bottom and the vegetation-free sand were separated by a belt of Zostera. Some areas of Zostera occurred intermingled with the sand and some areas without vegetation occurred in the Zostera-zone. In sectors A, G and H some parts were exposed at low water.

The macro-fauna of the sand was sparse. The most common species in the samples were Bathyporeia pilosa Lindström, Macoma baltica (L.), Mya arenaria L., Cardium lamarekii and Nereis diversicolor.

4) Zostera on sand constitutes the outer parts of all sectors except in the Malmö harbour. Its innermost limit is at a depth of about 1 m. The community of the Zostera-zone was dominated by Mytilus edulis L., Cardium lamarekii, Hydrobiidae spp., Litorina litorca (L.), Idothea viridis, and Gammarus sp..

5) Natural stony bottom occurs in restricted areas in sectors A-C and perhaps in parts of the Malmö harbour area. The algae vegetation on this bottom was rich and dominated by Fucus vesiculosus, Fucus serratus L., and various green algae such as Enteromorpha sp. The macro-fauna was dominated by Mytilus edulis. Also common were Gammarus sp., Idothea viridis, I. baltica, Hydrobiidae spp. and Theodoxus fluviatilis (L) but most species from the other bottom types were occasionally found.

6) Malmö harbour area comprises sectors H(partly)-N. Large areas of the bottom are covered with stones together with silt and other material dumped into the sea by man. Thus large parts of sectors J, H, L and N have been raised from a depth of about 6 m to 4 m. Consequently the bot-



tom is a mosaic of the dumped material and the natural bottom with stony areas and Zostera-meadows. The natural stony bottom is especially widespread in sector N.

The rich algae vegetation was partly caused by the discharge of untreated sewage from the city of Malmö in the northern part of sector N and of treated sewage in the outer parts of sector H. Fucus vesiculosus and F. serratus formed dense stands but Enteromorpha sp. took a dominating position near the outlet.

The fauna was rich consisting of the typical Zostera-community in the parts dominated by Zostera and a community dominated by Mytilus edulis, Hydrobiidae spp., Gammarus sp., Idothea viridis, I. baltica, Litorina littorea and Theodoxus fluviatilis on the stony parts.

This area undoubtedly had the richest bottom fauna of the whole study area but quantitative samples could not be taken. Qualitative samples were taken with a Birge-Ekman grab sampling 0.02 m². Maximum numbers in one grab were 850 Hydrobia (42,500 /m²) and 198 Mytilus edulis (10,000 /m²). The counts were certainly much too low as the grab did not take all material in the sampled area.

Besides the marine areas described above, three ponds (F, K and V in Fig. 2) near the coast were included as they were used by the ducks for resting. The invertebrate fauna of the ponds was not studied as they were not used for feeding.

South coast

The bottom types of the south coast and its fauna were studied by dredging from small boats in the area with a depth of less than 6 m with complementary dredgings in deeper water from the research vessel of the Zoological Institute in November 1967. Owing to the stony bottom quantitative samples were not obtainable.

The shore is mainly composed of stony areas and sandy beaches (Fig. 3). The bottom is stony up to the shore in all areas except just off the beaches where it consists of sand that gradually becomes coarser and mixed with gravel until the stony bottom appears 300-500 m from the shore. Some patches of sand and gravel occur intermingled with the stones.

The algae vegetation of the stones was rich and dominated by Fucus vesiculosus near the shore and F. serratus in deeper water. Various red algae, e.g. Ahnfeldtia plicata (Huds.), Furcellaria fastigiata (Huds.) and Ceramium sp. were also common on the gravel as were Enteromorpha sp. and other



green algae. Zostera marina was sparse.

The macro-fauna was dominated by Mytilus edulis both on the stones and on gravel and coarse sand. The different algae, especially Ahnfeldtia plicata, were important substrates for Mytilus and also harboured large quantities of Gammarus sp. and Idothea baltica. These three species dominated the fauna in the whole area markedly and occurred in large quantities. Other dominating species on the stony bottom were Idothea viridis and Litorina litorea. On the gravel and coarse sand Mysidacea spp. and Crangon crangon L were also common. The vegetation-free sand had a sparse macro-fauna including Macoma baltica, Cardium lamarekii and Mya arenaria (cf. also Table 1).

Sölvesborg area

The area consists of a bay that also includes the harbour of the town Sölvesborg (Fig. 4). Outside the bay there is a small low moraine island and a group of skerries. The shores are generally stony except in the inner parts and have some boulders. In the innermost parts of the bay there were some reed beds (Phragmites communis Trin.). The bottom is varied with stony areas mixed with areas of sand or mud. Stones also occur in the sand.

The vegetation of the stony areas was dominated by Fucus vesiculosus and F. serratus together with red algae, e.g. Ahnfeldtia plicata, Furcellaria fastigiata and Ceramium sp. and green algae, e.g. Enteromorpha. The fauna of these areas was rich and dominated by Mytilus edulis, Gammarus sp. and Idothea baltica (Table 1).

The muddy bottom had a vegetation of Potamogeton pectinatus L., Ruppia sp. but some Zanichellia palustris were also found. Zostera marina formed meadows only in small parts of the area. The bottom fauna of the muddy areas was dominated by Hydrobiidae spp., Cardium lamarekii and Nereis diversicolor that were all very abundant. The Zostera-meadows had the typical fauna of that habitat (see above!).

3. Weather characteristics of the studied seasons

1964/65 was a rather normal season with only little ice formed around the coasts in January and February. March was cold, and extensive ice formed around the coasts in the Öresund between the 3rd and 17th with only small areas open. The south coast had no ice that winter.

1965/66 was characterized by numerous cold periods with the first ice appearing in the second week of November. Extensive ice formed around the

coasts. On the south coast a belt of drifting ice lay off the shore for about 1-2 km between January 30 and March 5 with some ice in early January. The area in the Öresund was covered with extensive ice between February 15 and March 10 but some ice formed in the beginning of January.

1966/67, on the other hand, was mild with no ice formed around the coasts and an early spring.

1969/70 was a cold winter with most parts of the areas in southwest Scania covered with ice from early February to mid March. In the Sölvesborg area the inner parts were frozen from early December to late March and from mid February to mid March only small areas were free from ice.

4. Composition of the diving duck populations

Counts of the resting and wintering ducks were made simultaneously with the mapping tours in the study areas in southwest Scania at least twice a month during September (October for the south coast in the first two years) - April in 1964/65-1967/68 and once a month in 1968/69 and 1969/70 (Tables 2 and 3). Counts in the Sölvesborg area were only made in 1969/70 (Table 4). These data are presented here to serve as a background for the discussions below and the counts in Scania will be discussed in detail elsewhere (Nilsson in prep.). The duck populations outside the study areas were surveyed by boat (Table 5).

5. Local distribution of the species in the study areas

Methods

As it was not possible to observe all ducks from land two different methods were used to delimit their daytime distribution and a third method was used to find their night-quarters.

a) Counting and mapping tours from land were made about twice a month from September to the end of April in each study area that could be covered in one day. Counts were made from fixed points in the sectors (Figs. 2 and 3) so situated that the whole area between them could be surveyed by telescope (40 x 60). The positions of the observed groups were entered on large scale maps. Besides numbers, activity and sex-ratio were also recorded. It was possible to map the distribution of all ducks in shallow water (0-6 m), i.e. all Scaups, Aythya marila (L.), Tufted Ducks, Aythya fuligula (L.), Pochards, Aythya ferina (L.), Goldeneyes, Bucephala clangula (L.), Goosanders, Mergus merganser, L. and Snows, Mergus albellus L.. Almost all Eiders, Somateria mollissima (L.) could be seen as could a



large proportion of the Long-tailed Ducks, Clangula hyemalis (L.), and Red-breasted Mergansers, Mergus serrator L., whereas only occasional Velvet Scoters, Melanitta fusca (L.) and Common Scoters, Melanitta nigra (L.) could be seen.

85 mapping tours were made to the Öresund area and 56 tours were made to the south coast in 1964/65-1966/67. Moreover, data from 50 counts in 1962/63-1963/64 from the Öresund area and 31 counts from both areas in 1967/68-1969/70 were available. 12 counts were made in the Sölvesborg area in 1969/70.

b) Censuses at sea were made in 1965/66 and 1966/67 during the ordinary patrols of the Swedish Coast Guard to map the distribution of the ducks lying too distant from the shore to be seen through the telescope (Table 5). The censuses were made on predetermined courses permitting a good coverage of the water areas surveyed (Fig. 14). The position of the boat was determined by radar and the time for each position was noted on the nautical chart. All ducks were counted and recorded with time of observation on tape. The speed of the boats was generally 10 knots.

Since disturbed birds frequently moved forward in relation to the vessel there was a risk of double counting. All possible care was taken to avoid entering the flocks more than once.

Another factor of importance is the distance in which the ducks can be detected and accurately counted from the survey lines. For the Long-tailed Duck that is light coloured and sometimes difficult to spot on the sea this distance was estimated (by use of radar) to be about 700 m, whereas a Scoter on the water was seen 1500 m from the boat. This distance will vary with the weather conditions as will the reliability of the counts.

The records on tape were later transferred to survey maps using the time recordings on the tape and the charts. For the Long-tailed Duck the observations were summarized for 1 km of survey lines whereas the observations of the more sparse species were entered individually on the maps.

c) Observations on the evening flights to delimit the nighttime feeding areas of the Tufted Ducks and the Scaups and the resting places of the Goldeneyes could only be made in the Öresund area where the light evening sky provided a favourable background for the observations. They were made from suitable places near the daily resting or feeding places also using observation chains in radio contact.



The local distribution at the coast of SW Scandinavia of the different species

The discussion here will be restricted to the Öresund area and the south coast as the Sölvesborg area was only studied in one year that was characterized by much ice. The local distribution of the different species in the Sölvesborg area that winter was thus markedly influenced by ice. In the south coast study area the main part of the work was undertaken in the eastern part (A-H), that has the most varied shore and bottom conditions.

Scaup, *Anthus marila*

The Scaup was mainly restricted to the Öresund area with only few individuals counted on the south coast. They were generally concentrated to one main flock that stayed either at Habo (F) when the ponds were open or near the oil harbour of Malmö (H) when the ponds were frozen (Fig. 5). In spring the Scaups arrived at Habo before the ponds were open and then stayed at the sea in the southern part of sector E.

In the autumn they were mixed with the Tufted Ducks but in spring, when the Tufted Ducks were fewer and the Scaups commoner they concentrated in a flock of their own.

The ponds at Habo were used as resting places during the day and the Scaups made regular feeding flights together with the Tufted Ducks to Bjärred (D+E, Fig. 6) where they fed in the Zostera-zone. As was found from the stomach analysis (see below) they had not exactly the same feeding places as the Tufted Ducks.

In the oil harbour of Malmö the Scaups rested in one or a few flocks north of the harbour generally about 100 m from the shore, the exact place depending on weather conditions and the activities in the harbour. The feeding flights could not be followed here owing to observational difficulties but they seemed to make flights similar to those of the Tufted Ducks (Fig. 6). Some Scaups were seen feeding on Mytilus beds near the harbour and some Scaups were caught in nets together with Tufted Ducks 2-3 km N. of the resting places over stony bottom rich with Mytilus.

Thus feeding Scaups occurred in two restricted areas near the two resting places whereas large areas with similar bottom communities and suitable resting places (some being used by the Tufted Ducks) were not used by the Scaups. Their absence from the rich areas of sector N may be especially noted. It seems probable that the selection of resting places and feeding places in this species is an effect of tradition. The absence of Scaups from the south coast (Table 3) might be caused by a lack of suitable



resting places (however the Tufted Ducks had some in this area) but as the flock in the Öresund area was the only one of importance in Scania this absence was probably also related to tradition; the feeding grounds of the south coast had rich supplies of Mytilus edulis, the preferred food of the species.

Tufted Duck, *Aythya fuligula*

The Tufted Duck was the dominating diving duck of the Öresund area where it was mainly night-active, spending the day on special resting places from which it made regular evening flights to the feeding grounds at sea (Figs. 6-8). It was also common on the south coast (Tables 3 and 6) but not so dominant. The Tufted Ducks in a sector were generally gathered in one or a few large flocks, often 1000-2000 or more individuals.

In the early autumn the Tufted Ducks of the Öresund area concentrated to three resting places, i.e., the ponds F, K and V (Fig. 9). These three flocks dominated in autumn until the first main frost when new Tufted Ducks arrived in large numbers and flocks appeared in M and N. When the ponds freezed, the flocks shifted position and resting flocks appeared in the outer parts of the harbour and in some other sectors.

During the winter months the positions of the flocks shifted according to the ice conditions but the Tufted Ducks remained near their normal resting places, even during the hardest periods as long as some open water was available. During the ice periods the ducks moved to places not normally used and in February 1966 7,000 were counted at Sibbarp (RS).

In spring the Tufted Ducks disappeared early from all places except the favoured ponds (F, K and V). Numbers were generally low except at Klagshamn (V) where some hundred individuals were counted in May. At Habo (F) the flock appeared before the ponds were open and stayed at sea for a period.

It was not possible to follow all feeding flights to their full extent but the general localization of the main feeding areas could be deduced from those followed and from other observations (Figs. 6-8). At Habo (F) the flocks showed a consistent flight direction to the NW with very little variation. The main feeding areas were situated in sector D and E where they were seen feeding both over the Zostera-meadows and the mud. Many were caught in nets here. In winter almost all not-caught specimens were taken over the Zostera whereas in the autumn and spring they were mainly caught over the mud.

The Tufted Ducks at K, L and H took a northerly direction to feeding areas



in sector H and G (Figs. 6 and 7). Tufted Ducks were commonly caught in nets 2-3 km north of the resting places over a bottom rich with Mytilus, some were also seen to feed on Mytilus near the oil harbour at H.

From M the flocks always took a straight course to the northern parts of sector N with its rich Mytilus beds. The flocks resting at N generally dispersed over the area only and sometimes stayed over the feeding areas all day. Regular flights along the shores of the sector were seen in the mornings to the resting places.

The flock at V always held a steady course to the SW passing over the same group of buildings. Following the course one arrives at extensive shallow areas in the Öresund south of Klagshamn rich in Mytilus. The same areas were probably used by the Tufted Ducks from the Falsterbo Canal south of Klagshamn (Fig. 8).

The resting places used by the Tufted Ducks in the Öresund were thus all situated in sheltered positions. From these the ducks moved to feeding grounds at sea showing great persistence in the direction of the flights. The feeding quarters could not be mapped exactly but it is clear from the evidence gathered (Figs. 6-9) that important areas were not regularly used by the Tufted Ducks e.g. most areas between Limhamn and Klagshamn (P-S) that were only used during heavy ice periods and Saltviken (A), where the bottom community (Zostera for most parts, Fig. 2) was as rich as in many areas used by the ducks elsewhere. The most favoured areas near the Malmö harbour (G-N) had, however, the richest bottom communities in the Öresund area with abundant Mytilus. Moreover, many suitable resting places in sheltered positions were available in the harbour (Fig. 7).

On the south coast the Tufted Ducks were also concentrated to a few areas, the same each year (Table 6). The lower number of Tufted Ducks on the south coast as compared with the Öresund area (Tables 2 and 3) was probably related to the more open character of the south coast with few resting places suitable for large flocks, the food supplies being sufficient. However many places similar to those used had no Tufted Ducks.

Tradition seems thus important for the local distribution of the Tufted Duck, a suggestion that is strengthened by the regular pattern of appearance in the different sectors and the fixed positions of the resting places and flight directions. The ultimate factors involved are probably suitable resting places with good feeding grounds nearby but in an area richly supplied with both tradition will have an important influence on the local distribution.

Pochard, *Aythya ferina*

The Pochard occurred in small numbers in the study areas. The only concentration was found at K in the Öresund area where the majority of the Pochards in the area were resting together with the Tufted Ducks making regular feeding flights to sea together with the Tufted Ducks. Pochards were mainly absent from the other resting places used by the Tufted Ducks so tradition was probably involved.

Goldeneye, *Bucophala clangula*

In the Öresund area the Goldeneyes fed during the day in small, well dispersed groups and a few larger flocks of up to 50-100 individuals (at N). They preferred shallow water (3 m) but over the rich areas in sector N they were found to feed in deeper water (Fig. 10). All bottom types were used except pure sand but they were concentrated over stony bottom in sector ABC, over the mud and inner Zostera-belt in sectors D+E and over the areas in the Malmö harbour with a rich fauna on dumped stones. During ice periods the Goldeneyes were forced to leave the favoured areas but as far as possible they remained in the few open areas available or moved to the edge of the ice.

The Goldeneyes in the Öresund area showed a different distribution in the different months (Fig. 11). During early autumn most Goldeneyes (still only few had arrived) were concentrated to Saltviken (A) probably because most other areas were much disturbed by small boats. Later in the autumn and in the winter a large proportion of the Goldeneyes occurred in sector C-E especially over the muddy bottom and the inner Zostera-zone. Goldeneyes were also common in winter over the rich stony areas in the Malmö harbour (J-N). In the other areas, few Goldeneyes were counted on most occasions even if these areas had equally good food resources as the Habo-Bjärred area (D-E).

A detailed mapping of the distribution of the Goldeneyes was undertaken in Saltviken (A). The distribution of feeding Goldeneyes was marked on large scale maps and the totals for the four bottom types were calculated. A marked preference (significant for $P < 0.001$) was found for shallow waters with stony bottom and a rich fauna (Table 7).

The localization of the resting places in the Öresund study area was studied on 61 evenings. The majority of the Goldeneyes gathered in the evenings at common resting places which were situated at the same sites each year. All resting flocks stayed well out at sea (Fig. 10). Some irregularities occurred in the early season when the first arrivals in a sector moved to

the resting place of a neighbouring sector where the species was more common.

Similar evening flights in the Goldeneye were reported from North America and England (Breckonridge 1953, King 1961, Linsell 1969) whereas Carter (1958) found that resting Goldeneyes in an area in New Brunswick were scattered in small groups at night and gathered in large flocks for feeding during the day.

On the south coast 30 % of the Goldeneyes in daytime were feeding in flocks of 50-100 individuals with a further 25 % in flocks of 25-50 individuals. A strong preference for prominent stony tongues of land with boulders and other stony shores was found whereas sandy beaches were generally avoided (Fig. 12, Tables 8 and 9). The preference for stony areas was probably related to the greater productivity of the Fucus-region compared with other bottom types. The preference for prominent points over other stony areas might be related to the better view obtained outside a point as compared with a straight shoreline. Moreover, the flocks were more visible here to other Goldeneyes passing by.

Some differences in the distribution of the species in the different months were found (Fig. 13). The area Abbekås-Hörte (G-H) generally had a larger proportion of the Goldeneyes early in the autumn than during winter and spring, whereas sector A-B had few Goldeneyes in early autumn. These differences between different months could not be related to differences in disturbance etc.

No larger evening flights were seen on the south coast. The flocks generally rested at sea at the same places as they were feeding but somewhat further out at sea.

Thus the Goldeneyes used most shallow areas in the two study areas except where the bottom consists of vegetation free sand. Some concentrations occurred over the most productive bottom types, but some areas with similar bottom type (and food resources) had only few Goldeneyes so tradition might be of importance. It was certainly involved in the localization of the resting places and in the appearance each winter of flocks of almost the same size in certain areas with few Goldeneyes in neighbouring areas.

In the Öresund area feeding Goldeneyes were generally restricted to depths of less than 3 m, whereas on the south coast the Goldeneyes were commonly feeding at depths of up to 6 m. This was probably related to the occurrence of much larger areas of very shallow water in the Öresund as

compared to the south coast where the shallowest areas may be too close to shore for this rather wary species.

Long-tailed Duck, *Clangula hyemalis*

The distribution of the Long-tailed Ducks in the waters around Scania was surveyed from both land and boats and four concentration areas with flocks of varying sizes up to some hundred individuals were found (Fig. 14). All areas have either stones or gravel on the bottom with a rich-Mytilus supply or sandy bottom with plentiful Macoma baltica. The depth normally varied between 5 and 15 m but Long-tailed Ducks were also seen on deeper water (up to 22 m).

The shallow areas at Falsterbo that were not used by the Long-tailed Ducks were sandy bottoms with a rich population of Macoma baltica, whereas the areas with Long-tailed Ducks were stony grounds with Mytilus edulis. In the Öresund few Long-tailed Ducks were counted but the area has large areas suitable for feeding Long-tailed Ducks with Mytilus in large quantities. According to local fishermen the species was more common in the Sound earlier. Their absence here might be related to the fact that they follow the Baltic coast during migration.

Velvet Scoter, *Melanitta fusca*

Velvet Scoters were seen almost exclusively during the censuses taken at sea and only occasionally and in small numbers from the shore. They generally occurred in flocks of moderate size (10-25) that were concentrated to parts of the surveyed waters with no Velvet Scoters in the Öresund (Fig. 15). They were mainly found in areas with depths of 7-25 m over stony bottom with Mytilus or over sand with Macoma baltica. The reasons for their absence from the Öresund is obscure as good feeding grounds were abundant here.

Common Scoter, *Melanitta nigra*

The Common Scoter was only seen in small numbers and generally associated with the Velvet Scoters. Most of them were counted off the south coast especially east of Ystad.

Eider, *Somateria mollissima*

Few Eiders were recorded from the boat censuses; almost all individuals in the surveyed waters staying quite near the shore, normally in depths of less than 6 m. In the Öresund area they clearly preferred stony areas with rich Mytilus-fauna but some were found over the Zostera-meadows or in more shallow water (Table 10). The same preference for stony bottoms,

especially with stones in the waterline near protruding points, was found on the south coast (Table 11) and was certainly related to the rich abundance of Mytilus edulis here.

Red-breasted Merganser, Mergus serrator

The Red-breasted Merganser was mainly restricted to the south coast with small numbers seen in the Öresund and Hanöbukten (Fig. 16, Tables 2-3). On the south coast it was fairly evenly distributed except for an area west of Trolleborg and was found over all bottom types out to a depth of ca 15 m. The depth is not of the same importance in this fish-eating species as in those discussed above.

The flocks were generally small, under 10, with the maximum observed being 65. Most Red-breasted Mergansers occurred singly or in pairs.

No observations were obtained on the resting places of the species. After the arrival at the breeding places the Red-breasted Mergansers congregated at common resting places as do the resting flocks in spring (Curth 1954, Nilsson 1965).

The reasons for the low numbers seen in the Öresund are not clear as the Red-breasted Merganser can take a wide variety of fishes, crustaceans and polychaetes that occur in the Öresund (Madsen 1957). Geographical reasons were probably not involved as the species was also common in NW Scania. Tradition might be of importance.

Goosander, Mergus merganser

The Goosanders preferred inland waters and only appeared in numbers at the coasts when the lakes and inland streams were frozen. During the stay in the coastal waters they remained close to the shore and were not observed at sea during the boat censuses.

On the south coast the Goosanders were mainly concentrated to some marked stony points or stony shores (Table 12, Fig. 17) where they mainly occurred in discrete flocks of moderate size (10-60) that preferred resting places with good visibility in all directions. They mainly fished in the Fucus-zone among the stones where they were seen to take Anguilla anguilla L., Cottus sp. and Zoarces viviparus L. (cf. Madsen 1957), Anguilla probably being most important.

The Goosanders in the Öresund area also had a markedly discontinuous distribution (Table 13) with about 50 % (except in 1965/66) concentrated to a stone heap in sector C about 1 km from the mouth of the River Kävlingeån. A flock of up to 120 individuals stayed here all winter making feeding expeditions mainly to the mouth of the river and the neighbouring

shallow areas. Also in other areas of the Öresund the Goosanders occurred mainly near stones in the water such as the break-waters in the Malmö harbour.

Thus the local distribution of the Goosander seems mainly to be governed by the availability of suitable resting places with good visibility in all directions, preferably emergent stones in the water, and good fishing grounds nearby. Tradition is apparently of importance in this species that used the same resting places each year, especially as some areas that seemed suitable had only few Goosanders.

Smew, *Mergus albellus*

The Smew was almost exclusively recorded in the northern part of the Öresund study area (A-L). A large proportion of the observations were made on the two ponds F and K and in the sheltered area L on the sea near K (Table 14). Other areas used were the river mouths at C and H. In 1968/69 and 1969/70 many new ponds were created in the Malmö harbour (M) and the majority of the Smews concentrated here, the total numbers being much higher in the Öresund study area than earlier. Thus the Smews prefer fresh water habitats and will only use more sheltered marine areas in periods of ice.

In the winters 1968/69 and 1969/70 some observations were made on the resting places of the Smews in the Malmö area. Generally they assembled in flocks on the feeding grounds in the evening but on at least one occasion they were seen to make a feeding flight to another part of the harbour.

6. Food choice

Methods

The work was concentrated to the bottom feeding species, and the fish-eating mergansers were omitted as it was not possible to compare their diet with the available food resources. Ducks were collected in six areas: Habo-Bjärred (D-F) and S. Lomma (G) in the Öresund, Gislöv (R-S), Abbekås (F-G) and Ystad (A) on the south coast and Sölvesborg.

The material of stomachs containing food comprises 32 Scaups, 145 Tufted Ducks, 4 Pochards, 62 Goldeneyes, 156 Long-tailed Ducks, 14 Common Scoters, 5 Velvet Scoters and 18 Eiders. All except some Tufted Ducks that were drowned in fishing nets were shot.

The gizzard and the oesophagus of the collected birds were removed and preserved in 80 % alcohol and their contents analysed separately. The

oesophagus contents were sorted according to species and weighed after drying between filter papers. The gizzard contents were well distributed over a pan and the proportions of the various food items in tenths of the total gizzard content were estimated. From these estimates the percentage composition of the diet was calculated.

Earlier studies have used somewhat different methods. Cottam (1939) separated the various food items and calculated the percentage by volume for each as did Olney (1963) and Olney & Mills (1963) who also recorded frequency of occurrence. Madsen (1954) used frequency of occurrence and the frequency of the food item as the sole content of the stomach. Pethon (1967) counted actual numbers of all food species in the oesophagus and gizzard.

A factor of great importance when analyzing stomach contents of birds shot is the differential rates of digestion for various food items and the fact that digestion continues after the bird is dead (Jensen & Korschgen 1947, Koersveld 1950, Pollard 1967). In the present study the food of the ducks mainly consisted of bivalves, gastropods and crustaceans with a few polychaetes. Polychaetes leave only bristles and jaws, whereas crustaceans leave larger identifiable fragments. Molluscs leave more persistent fragments but variations occur: Litorina leave almost intact columellas whereas Hydrobia is often ground to a sandy appearance.

Therefore the analysis of stomach contents will give different results according to the time that elapsed between the last meal and death. In individuals shot just after feeding analysis of the gizzard contents will reveal almost the true composition of the meal but after some time only the resistant species will persist in identifiable fragments. Volumetric measurements and weighing will thus be difficult and will not yield reliable estimates of the composition of the diet, especially as in most cases, when the gizzard is filled with a mixture of well-ground fragments that are almost impossible to separate. The numerical method by Pethon (1967) will also give rather uncertain results as the sizes of the various food items can hardly be estimated and individuals are often not possible to separate. In many stomachs part of the content will be possible to identify by the colour of the fragments even when they are well ground (e.g., Mytilus edulis) but the fragments will not be possible to separate into individuals, whereas the harder fragments of another species will permit counting of the numbers taken. In view of the difficulties affecting the various methods the simple technique of gizzard analysis used here was regarded as sufficiently accurate to illustrate the composition of

the diet.

A more detailed knowledge of the diet would probably be obtained if the contents of the oesophagus were used instead of gizzard contents but most of the ducks had no food in the oesophagus but had well filled gizzards. When comparing the composition of the diet obtained from gizzard analysis according to the method described above with the weight-composition of the oesophagus contents of the same individuals no significant differences were found.

The food of the species investigated

Scaup, *Aythya marila*

24 specimens (almost all well filled) from the Öresund area shot in March-April 1967 and 1968 during the morning flight from the feeding grounds at Bjärred (D+E) to the resting place at Habo (F) showed a marked dominance for *Mytilus edulis* and *Macoma baltica* in the food (Fig. 18). One bird contained *Cardium lamarckii* in large numbers and one bird had fed almost exclusively on grains of barley (*Hordeum* sp.) probably taken from inland fields. The food in each specimen generally consisted of one dominating food item plus others more occasionally taken. Besides the dominating food-items the following were also found in moderate numbers in some stomachs: undet. *Bivalvia*, *Litorina* sp., *Hydrobiidae* spp.. Moreover a few specimens of *Mya arenaria*, *Gammarus* sp., *Idothea viridis*, *Crangon crangon* and some plant remains were found in single birds.

Three specimens had food in the oesophagus: one had 5.6 g of *Macoma baltica*, one 18.3 g of barley (*Hordeum* sp.) and 1.4 g of *Mytilus edulis* whereas the third contained 13.2 g of *Mytilus*, 1.5 g of *Litorina litorea* and 0.8 g of *Hydrobiidae* spp..

Eight stomachs from Sölvesborg in December 1966-70 (Fig. 18) showed a dominance for *Mytilus edulis* also containing *Macoma baltica*, *Mya arenaria*, plant remains, undet. bivalves and *Hydrobiidae* spp. in good numbers. More rare food items included polychaetes (probably *Nereis diversicolor*), *Cardium lamarckii*, *Litorina* sp. and seeds of *Scirpus*.

The composition of the food showed a high proportion of *Mytilus edulis* for the Bjärred area which is consistent with a feeding on the *Zostera*-bottom, where *Mytilus* was the dominating mollusc (cf. Nilsson 1969 a).

Madsen (1954) found a marked dominance for *Mytilus edulis* in Scaups from the Danish side of the Öresund with *Macoma baltica* as the second commonest food species, i.e. the same as was found in the present study. *Mytilus*

edulis was also the commonest food-item in other parts of the Danish waters together with a variety of other bivalves. In other more distant areas other bivalves and gastropods were found to dominate the diet of the species (Campbell 1936, Cronan 1957, Dementiev & Gladkov (cited in Olney 1958), Munro 1941). The diet also included a vast variety of other marine organisms, even algae (Cronan 1957, Lynch 1939).

Tufted Duck, *Aythya fuligula*

63 Tufted Ducks containing food were obtained from Bjärred (D+E) shot on the morning flights to the ponds at Habo (F) during September, November, December and March mainly in 1966/67. Four items made up almost the total food for the species in the Bjärred area: Mytilus edulis, Cardium lamarckii, Hydrobiidae spp. and Litorina litorea (Fig. 19). A similar composition of the diet was found in the few well filled oesophagus obtained (Table 15). In general one or two food items dominated the entire meal with the other items more occasionally found. Besides the dominating food items the following were also found in the stomachs: Mya arenaria, Macoma baltica, Theodoxus fluviatilis, Gammarus sp., Corophium sp., Idothea viridis, Cyathura carinata (one), Sphaerona sp., Balanus sp., Nereis diversicolor, Pisces (trace), Carex seed, Zanichellia seed and some unidentified plant remains.

A marked seasonal variation occurred in the food. In September Hydrobiidae spp. and Cardium dominated. Later in the season Mytilus edulis was more common and dominated in December, whereas Hydrobiidae spp. again dominated in March. Cardium lamarckii had a much lower share in the food in March than in the other months but it was commoner than Hydrobiidae spp. on the feeding grounds in April (Nilsson 1969 a). The diet of the Tufted Duck in September and March corresponded with the bottom fauna of the muddy areas at Bjärred, whereas the diet in December corresponded with the mollusc fauna in the Zostera-zone.

18 specimens drowned in fishing nets at Lomma (G) were obtained from December 1965 showing a marked dominance for Mytilus edulis and a good share of Hydrobiidae spp. and Litorina litorea in the food (Fig. 19). This corresponded well with the composition of the molluscanfauna of the area. The stomachs also contained the following items in small numbers: Cardium lamarckii, Mya arenaria, Theodoxus fluviatilis, Gammarus sp., Idothea sp. and a few plant remains.

29 Tufted Ducks were obtained from the south coast in March 1970 mainly shot over areas with stony bottom at Gislöv (R-S) and Ystad (A). The diet was markedly dominated by Mytilus edulis, the dominating mollusc of the

area, with Macoma baltica and Crustacea spp. taken in moderate numbers (Fig. 19). Other food items found were Cardium lamarekii, Mya arenaria, Gammarus sp. and barley (Hordeum sp.), that was certainly obtained from a nearby feeding place.

The diet of 31 Tufted Ducks shot at Sölvesborg in December (mainly 1969) was markedly dominated by Cardium lamarekii with Mytilus edulis as the second commonest species (Fig. 19). Cardium lamarekii was a dominant item of the soft bottom of the area as was Hydrobiidae spp. that was however only found in small numbers in a few stomachs. Other food items found included: Macoma baltica, Mya arenaria, Theodoxus fluviatilis, Litorina sp., Idothea sp., Gammarus sp., Pisces (trace), Scirpus seeds and Carex seeds.

In spring 1970 four Tufted Ducks were obtained from the area with a diet composited of Mytilus edulis, Cardium lamarekii, Macoma baltica, Hydrobiidae spp., Mya arenaria and Nereis diversicolor (Fig. 19).

Most oesophagi were empty, only some from the Bjärred area contained food (Table 15). The maximum content was 41 g. High counts of Hydrobiidae spp. were obtained from two oesophagi: 10,400 (28 g) and 12,000 (37 g) respectively.

A marked preference for molluscs in the diet is clear from the above. Generally the dominating mollusc of the area (usually Mytilus) dominated the diet. When there was a choice, e.g. in the Bjärred area and Sölvesborg the Tufted Ducks seemed to prefer Cardium lamarekii and Hydrobiidae spp. to Mytilus edulis but this might also be an effect of the different items occurring in different areas, Cardium and Hydrobiidae on the more shallow areas that might be preferred as feeding places.

Madsen (1954) found the food of the Tufted Duck in the Baltic and the Öresund to be dominated by Mytilus edulis, whereas Hydrobiidae spp. and Cardium were not so important. Tufted Ducks wintering in the southeast part of the Caspian sea fed almost exclusively on Cardium edule (Isakow & Worobjev 1950 cited in Bauer & Blotzheim 1969). A wide variety of food items have been recorded in small numbers in Tufted Ducks (Madsen 1954).

Pochard, Aythya ferina

Two Pochards obtained from Habo (F) contained unidentifiable plant remains probably taken in the ponds. Two Pochards from Sölvesborg contained Carex seeds and Mytilus edulis respectively. Pochards from brackish fjords in Denmark had mainly fed on plant food, especially seeds, but animal food was also taken (mainly molluscs) (Madsen 1954). Similar food choice was

recorded for Caspian Pochards by Isakow (in Dementiev & Gladkov 1952, cited in Bauer & Blotzheim 1969).

Goldeneye, Bucephala clangula

28 specimens were obtained from Sölvesborg in December (mainly 1969) and 21 from March-April 1970. In December Mytilus edulis constituted about 50 % of the diet with Pisces (some Gasterosteus sp.) undet. Crustaceans, Idothea (mainly baltica), Cardium lamarckii and undet. bivalves in some stomachs (Fig. 20). Moreover the following food-items were found in small numbers: Gammarus sp., Nereis diversicolor, Hydrobiidae spp., Theodoxus fluviatilis, Litorina sp., Macoma baltica, Mya arenaria and seeds of Carex and Ruppia.

In March-April polychaetes (probably all Nereis diversicolor) constituted 61 % of the food with only 27 % Mytilus edulis (Fig. 20). Some specimens also contained small numbers of Cardium lamarckii, Mya arenaria, Idothea viridis and some plant remains.

12 Goldeneyes from Ystad (A) on the south coast in March 1970 contained mainly Mytilus edulis with moderate amounts of Gammarus sp., undet. Crustaceans and polychaetes (probably Nereis diversicolor) (Fig. 20).

One Goldeneye was obtained from the Bjärred area with the stomach well filled with 3/5 Crustacea (Idothea viridis and Gammarus sp.) and 2/5 Hydrobiidae spp.,

The main food of the Goldeneyes from Öresund and the Baltic according to Madsen (1954) was various molluscs (e.g. Mytilus edulis, Hydrobia sp., Litorina sp.) and crustaceans (e.g. Gammarus sp. and Idothea sp.).

Crustaceans were also common in the diet of Goldeneyes from the Kategatt whereas seeds were common in stomachs obtained from brackish fjord areas (Madsen op.cit.). Olney & Mills (1963) found a great dominance for Carcinus moenas (L.) in the food of Goldeneyes from estuarine habitats in England. In the Caspian sea various molluscs and crustaceans dominated the diet (Isakow in Dementiev & Gladkov 1952, cited in Bauer & Blotzheim 1969). In North America crustaceans formed a large part of the food followed by molluscs (Cottam 1939).

Long-tailed Duck, Clangula hyemalis

31 specimens were obtained from the south coast in December 1966 and 1969. The food was markedly dominated by Mytilus edulis with Macoma baltica, Gammarus sp., Mysidacea spp., Idothea baltica, undet. crustaceans and fishes (partly Pleuronectes flesus L.) taken in smaller amounts (Table 16, Fig. 21).

Mytilus edulis was the dominating food item also in the 41 specimens obtained from the south coast in March 1966 and 1970 (Fig. 21). Smaller amounts of Mysidacea spp., undet. crustaceans and polychaetes (mainly Nereis diversicolor) were also taken.

From Sölvesborg 72 Long-tailed Ducks were obtained in November-December (mainly 1969). Mytilus edulis and crustaceans (Gammarus sp. and Idothea, mainly baltica) were equally common in the diet (Fig. 21). Moreover some Cardium lamarckii and single specimens of Macoma baltica, Litorina sp., Pisces (trace) and Mysidacea spp. were found.

In April 1970 12 Long-tailed Duck from this area showed a diet dominated by Mytilus edulis and Macoma baltica with smaller amounts of Cardium lamarckii, Mya arenaria, undet. crustaceans and polychaetes (mainly Nereis diversicolor) also being taken (Fig. 21).

Madsen (1954) found a marked dominance for Mytilus edulis with some Macoma baltica and 1/4-1/3 crustaceans in the food of the Long-tailed Ducks in the Baltic. In saltwater localities in the Kattegatt Cardium spp. dominated over Mytilus. Molluscs and crustaceans were also found to dominate the diet of the Long-tailed Duck by Campbell (1936), Cottam (1939), McGilvrey (1967), Salomonsen (1950) and Siivonen (1941).

Velvet Scoter, Melanitta fusca

Five specimens were obtained from Sölvesborg. Four were entirely filled with fragments of Macoma baltica and the fifth contained only Mytilus edulis. According to Madsen (1954) these species dominated the food of the Velvet Scoter in the Baltic whereas the diet was more varied in the Kattegatt.

Common Scoter, Melanitta nigra

One bird from Sölvesborg was completely filled with Mytilus edulis. 13 specimens obtained from the south coast had Mytilus edulis and Macoma baltica as the only food items except for a single specimen of Hydrobia (Fig. 22).

A marked dominance for bivalves, especially Mytilus edulis in the diet of the species was found by Madsen (1954). As in the other species the diet was more varied in the Kattegatt but bivalves still dominated. Molluscs were the main food for American Scoters studied by Cottam (1939) and McGilvrey (1967).

Eider, Somateria mollissima

18 Eiders from the south coast and Sölvesborg showed a marked dominance

for Mytilus edulis in the diet with Idothea baltica as the only other food item recorded (Fig. 23).

Earlier studies (Bauer & Blotzheim 1969, Cottam 1939, Flint 1955, Gerasimova & Paranova 1960, Madsen 1954, Pethon 1967, Pretsov & Flint 1963, Scot-Ryen 1941 and Segerstråle 1947) showed that the Eider take a variety of marine organisms as food but Mytilus edulis was the dominant food item when available.

Summary of food choice

From the data presented here and in the earlier studies referred to above, it is clear that the diving ducks are not restricted to any special kind of food but will readily take a wide variety of marine organisms. In effect most species recorded in the bottom fauna of the study areas may also be found in the stomachs of the diving ducks.

Mytilus edulis was the dominant food item in all species obtained in sufficient numbers to be analysed in the present study but some variations occurred. Mytilus was also the dominant species in the macro-fauna of all but rather small parts of the study areas.

In Scaups at Bjärred Macoma baltica was taken in numbers by some individuals in an area rich in Mytilus. In the Tufted Duck Cardium lamarckii and Hydrobiidae spp. dominated over Mytilus in the Bjärred area and the Sölvesborg area in some months. This was probably related to a preference to feed in the more shallow areas, where these species are the commonest molluscs. It may be noted that in March at Bjärred the Scaups mainly fed on Mytilus in the Zostera-zone, whereas the Tufted Ducks fed on Cardium and Hydrobiidae spp. on the muddy areas.

In both the Goldeneye and the Long-tailed Duck Mytilus edulis was the dominant food item in the Baltic but both species took quantities of more motile animals such as crustaceans and also polychaetes and some fishes. The Scoters and the Eider in the Baltic mainly relied on Mytilus and Macoma (the Scoters).

7. Diving habits

The Diving ducks take most of their food by diving for it. They usually search intensively for food with consecutive dives separated only by short pauses for rest. After feeding in that manner for some time the intensity decreases and longer pauses follow, often with preening or rest. In the coastal areas practically no food was obtained by any other method except during cold periods when the ducks were artificially fed by seed. The fish-eating mergansers have two different methods for food-seeking:

a) they make a series of consecutive dives like the bottom feeding species, b) they swim with the head partly under water and dive when discovering a prey.

To study the variation in the duration of dives and pauses during intensive feeding single diving ducks were selected and the duration of the consecutive dives and pauses in a series was timed to the second with a stopwatch. Measurements were taken on ducks over different depths. The mean duration of dives and pauses was calculated for each series as was the quotient between the total diving time and total pause time, i.e. the dive/pause ratio (cf. Dewar 1924).

Owing to the shallowness of the sea in the study areas it was not possible to obtain measurements from water deeper than 7 m for any species. The flocking behaviour of the diving ducks made it very difficult to get measurements on Scaups and on Tufted Ducks and Goldeneyes on deep water. The dives on depths less than 1 m were measured over muddy bottom whereas the other dives were measured over stony areas in the Öresund area and on the south coast.

The diving depth

Scaups were seen to dive to depths of 5-6 m but Dewar (1924) recorded dives of up to 8 m. The preferred depth is however lower (cf. Cronan 1957).

Tufted Ducks were commonly seen to dive to depths of about 7 m as was also found by Dewar (1924) and Huber (1956) but on inland waters in Scania they were obtained in nets at a depth of 11 m and diving depths of up to 14 m have been recorded (Wereschtschagin according to Bauer & Blotzheim 1969). According to Bezzel (1959) the females seem to prefer more shallow water than the male as was also found in the Pochard. No such difference between the sexes was found in the present study but both species were night-active in the area and it might be missed. Differences in sex-ratio between different resting places in the Tufted Duck were found by Nilsson (1970 a).

Pochards were mainly seen to dive in shallow water less than 2 m deep but Huber (1956) recorded a maximum depth of 4.5 m (cf. also Bauer & Blotzheim 1969).

Goldeneyes were commonly seen diving to depths of 6-7 m in the present study but Olney & Mills recorded dives of up to 9 m. Haartman (1945) stated that the sexes have unequal diving abilities the males diving deeper than the females. Nilsson (1970 a) found a different distribution

of the sexes on the feeding grounds with the males on deeper water further to the sea but it is not certain whether this was caused by real differences in diving ability (cf. below) or other factors. The females in this species are smaller than the males and have higher diving intensities (Nilsson 1970 b) and it is possible that they have to dive on shallow water, that is more economic, to obtain sufficient quantities of food, whereas the larger males can afford to stay on deeper water where the dives are less economic.

Long-tailed Ducks were seen diving to depths of 22 m but they have been taken in nets at depths of 60 m in the Great Lakes in North America (Ellarson 1956, Schorger 1947). Schmidt (1966) recorded dives to depths of 28 m on the Baltic coast of Germany.

The Scoters stay far out at sea and their diving habits could not be studied. During the boat censuses diving scoters were seen at depths of more than 20 m, normal depths being 10-15 m (cf. Bauer & Blotzheim 1969).

Eiders were mainly seen feeding in shallow water, i.e. less than 6 m deep, but dives on depths of 12-16 m have been recorded (Bergman 1939, Pethon 1967).

In the present study Goosanders were found diving to 5 m and Dewar (1924) recorded a maximum depth of 6 m, but in a fish-eating species it is difficult to establish the true diving depth.

Red-breasted mergansers were found over varying depths up to 15 m, but no measurements of dives were obtained.

In the Smew dives were recorded in depths of up to 2 m in the Öresund area but records of dives on depths of up to 6 m have been published (Meinertzhagen 1959).

The diving time

The duration of the dives was different in the different species. Long-tailed Ducks stayed under water much longer than Goldeneyes, Scaups and Tufted Ducks, whereas only rather small differences were found between these three species (Table 17). Individual differences in the dives were found but in general most dives were rather close to the mean of the depth interval.

Few studies have been published on the duration of dives of diving ducks in coastal waters. Dewar (1924) found diving times similar to those in the present study. For the Velvet Scoter and Common Scoter that could not be studied here he found mean diving times between 20 and 46 secs and 19

and 46 secs respectively for depths of 1-8 m. In the Scaup (Cronan 1957), Tufted Duck and Goldeneye (Haartman 1945) measurements similar to those obtained here have been published.

As discussed above Haartman (1945) stated that the sexes of the Goldeneye have different diving ability the males being superior. Mester & Prünke (1966) found longer diving times in the males than in the females for a locality in Germany whereas no such differences were found on the coasts of Scania or in inland Sweden (Nilsson 1969 b). The data of Willi (in Bauer & Blotzheim 1969) show differences in diving ability between the sexes in the Tufted Duck but as for the Goldeneye no such differences were found here.

In most species maximum diving times much longer than those found in the present study have been published but they are exceptional cases (cf. Anderson 1920, Bauer & Blotzheim 1969, Dewar 1924, Ingram & Salmon 1929, 1941).

The time-depth relation

The relation between diving time and depth was studied by Dewar (1924) who formulated a rule for this relation. The rule has however been criticized by Ingram & Salmon (1941) and Schorger (1947). Even if no absolute rule can be formulated, it is clear that a relation exists between the diving time and the depth (Fig. 24, cf. also Willi in Bauer & Blotzheim 1969).

In the present study it was possible to study the time-depth relation only in the Goldeneye and Long-tailed Duck. In the Goldeneye an almost linear relation was found for depths between 1 and 5 m. For more shallow water relatively shorter dives were measured than could be expected from the curve. This divergence may have different causes. The diving times for depths of 0.5-1 m were only slightly lower than could be expected whereas the difference was marked for dives in water not deeper than 0.5 m. This might be caused by different kinds of food taken as the dives were measured over different bottom types.

The curve for the Long-tailed Duck had a similar appearance but the bend of the curve occurred at greater depths. In this species some birds diving in shallow water might not have been in full health as individuals that were somewhat oiled gathered here.

When comparing the curves the better diving ability for the Long-tailed Duck compared to the Goldeneye is apparent. Similarly when comparing these curves with the curves for the Tufted Duck by Willi (in Bauer &

Blotzheim 1969) the Tufted Duck is found to be inferior to these two species.

The almost linear relation between diving time and depth for part of the curve might imply that for these depths the birds have a rather fixed bottom time in which to search for food, the increase in diving time being caused by increase in the time needed to reach the bottom and to return to the surface. This bottom time will be obtained if the almost straight parts of the curve are drawn out to the intersection with the ordinate.

In the present study the bottom time for the Goldeneye so obtained was 16 secs for depths of 1-5 m and for the Long-tailed Duck 18-20 secs for depths of 1-7 m. Using these values and the diving times and pauses in table 17 the effective feeding time during a series of dives was calculated. For depths of 1-2 m it was 57 % in the Goldeneye and 61 % in the Long-tailed Duck. At a depth of 2-3 m it was 50 % and 48 % respectively and for depths of 4-5 m 42 % and 40 % respectively. In shallow water the Goldeneye and Long-tailed Duck thus had the same effective feeding times.

It was not possible to calculate such data for the Tufted Duck as measurements were obtained for few depth classes only. Willi (op.cit.) calculated an effective bottom time for the Tufted Ducks in fresh water of 17 secs. for the male and 14 secs. for the female, but he presents no data on the length of the pause. For the Pochard he calculated a bottom time of 13-14 secs for shallow water. With a similar bottom time at the coasts of Scania the Tufted Duck will have a lower effective feeding time than the Goldeneye and Long-tailed Duck.

For deeper water deviations from the linear relation might be expected as the birds reach their upper limit for diving. In the present study no such data were obtained but Willi (op.cit.) found a deviation for the Pochard at a depth of about 3 m.

The dive-pause ratio

The different species were found to have different dive/pause ratios (Table 17). The highest ratio was noted for the Long-tailed Duck and the lowest ratios were found for the Scaup and the Tufted Duck (among the smaller species). Dewar (1924) calculated dive/pause ratios for a number of birds. For dives in shallow water (0-2 m) he found values similar to those obtained here except for the Goldeneye for which he obtained a ratio of 1.9. The Scoters had a ratio of 1.3. Dow (1964) found values similar to those published here for the Goldeneye and Long-tailed Duck.

One further aspect of interest is the relation between the length of the

pause and the length of the preceding dive. This might be used to obtain an indication of the longest economic duration of dives. A steady increase in the pause with longer dives might be expected up to a point where the slope of the curve becomes steeper as the birds need relatively longer pauses because of exhaustion. This point might be taken as an indication of the longest time for normal diving.

Such curves were calculated for the Tufted Duck, Goldeneye and Long-tailed Duck using mean values of the pause for each interval in diving time (Fig. 25). A good correlation for the whole register of measured dives was found for the Goldeneye but in a freshwater locality an exhaustion effect was noted (Nilsson 1969 b). The absence of this in the present material is probably related to the fact that no dives were measured for the greatest depths used by the species. In the Long-tailed Duck a change in slope was noted at about 45 secs. but this is far from the longest dives recorded, the less healthy condition of some specimens might have influenced the results. In the Tufted Duck a marked change in slope was found for dives of 26-30 secs.

When comparing the curves of the three species their relation to each other is the same as could be expected from the dive/pause ratios, the Long-tailed Duck being the most efficient diver of the three.

Summary on diving habits

From the preceding sections it is clear that the different species of diving ducks have different diving abilities. The smaller bottom feeding species (the Eider and the Scoters excluded) can be arranged in a series according to decreasing diving efficiency. The most efficient diver using all criteria is the Long-tailed Duck. The next species to follow is the Goldeneye. The maximum diving depth for this species was the same as in the Scaup and Tufted Duck but it had a higher dive/pause ratio. Similarly the Scaup had a higher dive/pause ratio than the Tufted Duck. The least efficient diver of the species considered was the Pochard that reached a maximum diving depth of about 4 m (cf. Willi in Bauer & Blotzheim 1969) and had a lower dive/pause ratio than the other species. Among the mergansers the Goosander had a higher dive/pause ratio and longer diving times than the Smew.

These differences in the diving efficiency were reflected in the local distribution of the different species. The Long-tailed Duck was the dominant species in off-shore waters, whereas the other species only fed in more shallow water near the shore. In the Öresund most feeding in the

Goldeneye was found to take place in water not deeper than 2-3 m except in the rich area of Ribersborg (N) and in cold periods but on the south coast they fed at depths of up to 6 m. In the night-active species the exact feeding places were difficult to locate but the stomach analysis of Scaups and Tufted Ducks from the Bjärred area in March showed that the Scaups had fed on the Zostera-zone, i.e. in deeper water than the Tufted Ducks that mainly fed on the muddy bottom. Differences in diving efficiency might also be responsible, at least partly, for regional differences in the distribution of diving ducks. During hard periods the less efficient divers will have greater difficulties in obtaining sufficient quantities of food than the more efficient divers especially as the shallow water where diving is most economic will be frozen. Other aspects such as the period for feeding will also be of importance in this connection. The marked dominance for Long-tailed Ducks in the Baltic during winter must be seen in this connection.

8. Exploitation of food resources

It is of particular interest to attempt an evaluation of the degree of exploitation of the food resources by the diving ducks. For this reason the exploitation in terms of bird-day units was estimated for the different species of bottom feeding diving ducks in different parts of the study areas. As it was not possible to establish the exact feeding areas of the night-active species, the whole counting sectors out to a depth of 6 m were used as units except for Habo-Bjärred (D+E) in the Öresund where all feeding was known to take place inside the 3 m depth curve. On the south coast the Long-tailed Ducks caused problems as they also fed on deeper water. A large part of those seen from the shore were however feeding inside the six metre depth curve and all Long-tailed Ducks seen from the shore are included as feeding in the area. The values for the south coast will thus be somewhat too high.

No exact measurements of the daily food intake are available for the species concerned. For the Eider a daily consumption of 300 g of molluscs fresh weight was estimated by Belopolski (1957) and Portsov (1951) cited in Geramisova & Baranova (1960). In captured Canvasbacks, Aythya valisneria (Wilson), and Lesser Scaups, Aythya affinis (Eyton), fed on a mixture of natural foods, mainly plants, the mean consumption in autumn was found to be 200-350 g, i.e. 30-40 % of their body weights (Longcore & Cornwell 1964). The Scaup, Tufted Duck, Goldeneye and Long-tailed Duck are of similar size and thus the mean daily food intake in the calculations here



was set to 200 g. The daily food consumption will however vary with the kinds of food taken and with the season so this estimate will only be a very rough one as will the figures based on it.

By using this value the food consumption per m^2 and year was calculated for the different sectors of the study areas.

In the Öresund area (Table 18) the exploitation varied from $0.1 \text{ g/m}^2/\text{year}$ to $29 \text{ g/m}^2/\text{year}$. The highest values were calculated for the Ribersborg area (N), that was especially rich. In general the values were low and below $10 \text{ g/m}^2/\text{year}$.

In the Bjärred area the calculated food consumption was compared with the standing crop of potential food species in autumn and spring (Nilsson 1969 a). The total food-intake of the diving ducks was about 5 % of the decrease in standing crop between November and April.

During the mapping of the bottom communities quantitative samples were taken in sectors A, D+E and S in April 1966 (Table 19). Owing to the method used (aiming at obtaining a general idea of the bottom communities) some food items were perhaps under-represented in the material. That applies especially to Gammarus and Idothea that might have been lost to some extent during the sampling and to Hydrobiidae spp. that were partly missed during the sorting in the field as was later found (1966/67) when the samples were brought to the laboratory to be sorted. Hydrobiidae spp. are thus excluded from the table as are some species occurring more patchily so the values in the table are minimum values.

The highest standing crop for Mytilus, the most important food item for the diving ducks, was found in the Bjärred area although the samples were taken after a winter when many diving ducks had been feeding there. For Cardium Bjärred showed a much lower standing crop than the Klagshamn area, but Cardium was a favourite food of Tufted Ducks that fed in good numbers in the Bjärred area but not in the Klagshamn area. In all areas the food resources were very good for the diving ducks.

The exploitation rates for the south coast sectors were of similar size-order to those from the areas in the Öresund (Table 20). It is especially interesting to compare the three sectors Ystad-Svarto (A-B), Abbekås-W. Hörte (G-H) and Stavsten-Kämpinge (U-X) as they all have stony bottoms with a similar fauna, probably with standing crops of similar magnitude. Even so the Stavsten-Kämpinge area was found to have a markedly lower rate of exploitation than the other two areas.

In the Sölvesborg area, finally, the following number of bird-day units



were calculated for 1969/70: Scaup 1,100, Tufted Duck 163,000, Pochard 4,000, Goldeneye 12,500 and Long-tailed Duck 32,400; total 213,000. The rate of exploitation was 2.5 g/m^2 and was certainly small in relation to the standing crop of potential food species. It must however be remembered that large parts of the area were ice-covered from late December to March so the rate of exploitation of the ice free areas was higher than the calculated figure.

In conclusion it was found that the highest rates of exploitation occurred in the richest areas. The degree of exploitation of the bottom fauna varied however much more than the food resources available. In areas with largely similar food resources markedly different rates of exploitation were found. In all areas the calculated exploitation was small compared to the standing crop of suitable food species and probably also in relation to the production of food species. Even if the calculated exploitation might have been too low it is clear that the food resources were sufficient for much larger numbers of ducks than now present.

9. Factors affecting the habitat selection of diving ducks in coastal waters during the winter season

The mechanisms of habitat selection of birds in general were reviewed by Hildén (1964, 1965). He separated three ultimate factors related to it: 1) availability of sufficient food supplies, 2) the structural and functional characteristics of the species, 3) protection against enemies and adverse weather conditions. The proximate factors, i.e. the environmental and internal factors that affect the instinctive process of habitat selection were also discussed by Hildén (op.cit.) who grouped them into characteristics related to 1) landscape, 2) topography, 3) sites of various activities, 4) other animals. The factors that govern the choice of places for various activities of ducks were also discussed by Szijj (1965).

In the winter the situation is simpler than in the summer as the two main activities of the ducks are feeding and resting so that the discussion may be restricted to the factors that govern the choice of feeding places and resting places.

It was found that the diving ducks usually collect only a small proportion of the total food resources available in normal seasons. The effect of the exploitation of the food resources by the diving ducks is reduced by their wide variety of food choice. Even if every species seems to have a certain preference they can readily feed on most bottom



species available. In the study areas there were, furthermore, large areas that had only few feeding ducks but almost as large food resources as the areas more heavily exploited by the diving ducks. The food resources around the coasts of Scania were thus adequate for the diving ducks and the food would have been sufficient for much larger numbers of diving ducks.

A more important factor than the total food resources present is the restriction on their availability for the different species depending both on the diving ability of the species and the environmental conditions. The effective feeding time is reduced with increasing depth and thus there is a limit to the use of the food resources in deeper water. This factor is especially important when the ducks are hard pressed and dive intensively for food. As the feeding intensity is increased in cold weather (Nilsson 1970 b) the ducks, especially those with a high normal feeding intensity, like the Goldeneye, can reach a limit when they cannot get enough food from the depths that they can use in more normal weather. The effect is increased by the ice that first covers the shallow areas. In such a species as the Goldeneye the margin is certainly not wide. In the Goldeneye the smaller females, that dived more intensively than the males, became outnumbered by the males in the coldest periods (Nilsson 1970 a).

Protection against enemies and adverse weather conditions is also a factor of importance for the habitat selection of diving ducks during the winter. The weather exerts its influence through the need for increased feeding intensity when it is cold, and through the ice that forces the ducks to leave their favoured places. Another factor of importance in this respect is the action of waves that will influence the selection of resting places in the Scaup and the Tufted Duck which for this purpose demand sheltered places. The feeding of the ducks seems not to be influenced by it.

The diving ducks at the coasts of Scania have few enemies. There were no predators of importance, and there was no hunting in the study areas. Moreover the ducks were well protected from terrestrial mammals on the water. In the Goosander and the Eider some resting places were situated on stones near the shore whereas most species rested on the water some distance from the shore.

In relation to protection the role of disturbance from human activities must be mentioned. Both study areas are situated in populated areas with considerable fishing activities etc. The Öresund area moreover includes

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the harbour of Malmö. In the Goldeneye the disturbed flocks abandoned their normal resting place, whereas the Scaups and Tufted Ducks often rested near busy places in the harbour as long as they were not disturbed on the water.

The proximate factors related to the habitat selection of diving ducks are more difficult to determine. Topographic factors are certainly of importance for the species staying near the shore as in the preference for stony points on the south coast, but the distance to land might also be a factor of importance e.g. in the Scoters.

The presence of other animals, in this case other diving ducks, is certainly important as the ducks are social animals usually occurring in large flocks. The sparser species such as Pochard and Scaup in autumn mixed with the numerous Tufted Ducks. In spring when the Scaups were more numerous they formed flocks of their own.

The concentration of ducks to certain places may also be seen in relation to this sociability: a flying flock is attracted to other ducks. This might explain the concentration of Goldeneyes outside certain promontories on the south coast.

A further important factor for the habitat selection of ducks is tradition. No other factor can explain the choice of the same resting and feeding places year after year in an area that provides many places of apparently equal quality. The rôle of tradition in the life of ducks was discussed in detail by Hochbaum (1960).

According to Lack (1968) the numbers of migratory species might be determined by the availability of food on the wintering grounds. Competition may lead to the development of differences in food choice and feeding habits among related species on the winter grounds. However the differences might be supposed to be small when food is abundant as was the case at the coasts of Scania.

The food choice of the bottom-feeding species was accordingly found to be rather similar with Mytilus edulis as the dominant food in all species. More important differences were found in the diving ability of the different species and they could be arranged in a series according to the diving ability. In relation to this the different species of bottom-feeding diving ducks have a different distribution when feeding although overlapping occurs (cf. Szijj 1965). Similar differences were also found in the fish-eating mergansers.

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Table 1. The composition of the macro-fauna of different bottom types in the study areas. +++ dominant, ++ fairly common, + found and - not found. Sampling by grabs in the Öresund area and by dredging on the south coast and in the Sölvesborg area. Samples taken in autumn and spring.

Species	Öresund						South coast		Sölvesborg	
	1 Mud	2 Sand + silt	3 Sand	4 Zost. on sand	5 Stones	6 Malmö harb.	Stones Gravel on sand	Sand	Stones Gravel Sand	Mud
<i>Mytilus edulis</i> L.	++	+	-	+++	+++	+++	+++	-	+++	+
<i>Macoma baltica</i> (L.)	++	++	++	++	-	+	+	+	++	++
<i>Mya arenaria</i> L.	++	++	++	++	-	+	+	+	+	++
<i>Cardium</i>										
<i>lamarckii</i> Reeve	+++	+++	++	+++	-	++	+	+	+	+++
Hydrobiidae spp.	+++	+++	+	++	++	+++	+	+	+++	+++
<i>Littorina (littorea</i> L.)	-	-	-	++	++	++	+++	-	++	-
<i>Theodoxus</i>										
<i>fluviatilis</i> (L.)	+	-	-	+	++	++	++	-	+	-
<i>limnea</i>										
<i>peregra</i> (Müller)	-	-	-	-	-	-	+	-	+	-
<i>residothea</i>										
<i>entomon</i> (L.)	-	-	-	-	-	-	+	-	-	-
<i>idothea</i>										
<i>viridis</i> (Slabber)	++	++	+	+++	+++	+++	++	-	-	-
<i>idothea</i>										
<i>baltica</i> (Pallas)	+	-	-	+	+	+	+++	+	+++	++
<i>lyathura</i>										
<i>carinata</i> (Kröyer)	++	+	+	+	+	+	-	-	-	-
<i>aera</i> sp.	+	+	-	+	+	+	+	-	-	-
<i>phaeroma</i> sp.	++	+	-	+	+	+	-	-	-	-
<i>ammarus</i> spp.	++	++	+	+++	+++	+++	+++	+	+++	++
<i>athyporeia</i>										
<i>pilosa</i> Lindström	-	+	+++	+	-	-	-	++	-	-
<i>orophium</i> sp.	++	+	-	+	+	+	+	-	+	+
<i>ysidacea</i> spp.	?	?	?	?	?	?	+++	+++	++	-
<i>crangon</i> L.	++	++	++	+	+	+	++	++	++	+
<i>ereis diversi-</i>										
<i>color</i> O.F.Müller	+++	+++	++	++	++	++	+	+	+	++
<i>armothoe</i> sp.	-	-	-	-	-	-	+	-	-	-
<i>iscicola</i>										
<i>geometra</i> (L.)	+	-	-	+	+	+	+	-	+	-
<i>hironomidae</i> spp.	+	-	-	-	-	-	-	-	-	-

Table 2. Monthly means of diving ducks in the Öresund study area 1964/65-1969/70 + occasional observation. Number of counts in brackets.

Species	Sept. (8)	Oct. (8)	Nov. (12)	Dec. (8)	Jan. (13)	Feb. (11)	March (14)	April (12)
<i>Aythya marila</i>	1	9	58	98	139	144	206	280
<i>Aythya fuligula</i>	614	2920	5250	7745	6940	7200	2380	1140
<i>Aythya ferina</i>	38	76	34	33	14	11	13	16
<i>Bucephala clangula</i>	43	106	556	982	1042	1221	1479	670
<i>Clangula hyemalis</i>	0	-	+	+	2	2	2	3
<i>Melanitta fusca</i>	0	0	+	0	+	+	+	0
<i>Melanitta nigra</i>	0	0	+	0	+	+	+	0
<i>Somateria mollissima</i>	211	91	82	27	28	43	55	66
<i>Mergus serrator</i>	21	48	21	10	4	5	7	26
<i>Mergus merganser</i>	3	4	16	68	137	193	50	12
<i>Mergus albellus</i>	0	+	4	21	16	16	12	4

Table 3. Monthly means of diving ducks in the south coast study area 1964/65-1969/70. + occasional observation. Number of counts in brackets.

Species	Sept. (4)	Oct. (7)	Nov. (10)	Dec. (9)	Jan. (12)	Feb. (13)	March (15)	April (11)
<i>Aythya marila</i>	0	+	2	12	7	7	6	1
<i>Aythya fuligula</i>	8	11	182	704	1105	1140	401	81
<i>Aythya ferina</i>	0	+	+	1	2	2	1	2
<i>Bucephala clangula</i>	102	105	670	1490	1730	1970	1085	402
<i>Clangula hyemalis</i>	0	+	106	607	774	1155	1110	252 ^{x)}
<i>Melanitta fusca</i>	0	0	+	1	2	3	6	+ ^{x)}
<i>Melanitta nigra</i>	0	+	+	+	1	4	4	3
<i>Somateria mollissima</i>	187	53	50	57	31	25	26	92
<i>Mergus serrator</i>	3	18	104	128	107	99	100	71
<i>Mergus merganser</i>	2	1	5	156	286	380	171	41
<i>Mergus albellus</i>	0	0	0	1	2	3	1	0

x) The springs of 1966 and 1970 not included as unusually large counts of resting flocks were obtained for some days.

Table 4. Mid-monthly counts of diving ducks in the Sölvesborg study area in 1969/70.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
<i>Aythya marila</i>	0	0	0	0	0	0	10
<i>Aythya fuligula</i>	820	760	640	1730	155	340	1140
<i>Aythya ferina</i>	10	5	27	8	0	0	140
<i>Bucephala clangula</i>	12	17	85	94	90	0	37
<i>Clangula hyemalis</i>	15	11	810	70	8	0	89
<i>Melanitta fusca</i>	0	3	0	0	0	0	0
<i>Somateria mollissima</i>	0	1	0	0	0	0	0
<i>Mergus serrator</i>	0	1	23	0	0	0	2
<i>Mergus merganser</i>	0	0	24	450	410	630	440
<i>Mergus albellus</i>	0	0	50	86	10	10	47



Table 5. Number of diving ducks counted on the boat surveys in the Scanian waters in 1965/66 and 1966/67. The geographical names and the survey lines will be found in Fig. 14. Duration of surveys (in hours) in brackets.

Date	Surveyed area	Clan. hyem.	Mel. fusc.	Mel. nigr.	Som. mol.	Merg. serr.	Merg. merg.	Merg. albel.
<u>1965</u>								
28.11	Simrishamn-Lägerholmen-Åhus-Sandhammaren-Simrishamn (7 h)	4294	69	1	21	-	-	-
1.12	Simrishamn-Kivik-Hanön-Lägerholmen-Simrishamn (7 h)	2069	20	-	4	-	-	-
13.12	Simrishamn-Smyge-Ystad-Simrishamn (7.5 h)	2011	139	24	75	35	9	-
17.12	Ystad-Sandhammaren-Abbekås-Ystad (5 h)	1131	181	-	8	64	2	1
<u>1966</u>								
17.1	Ystad-Kåseberga-Ystad-Abbekås-Smyge-Ystad (5.5 h)	2742	293	6	2	264	-	-
27.3	Simrishamn-Lägerholmen-Hanön-Åhus-Kivik (7 h)	1246	77	1	11	-	-	-
30.3	Ystad-Kåseberga-Sandhammaren-Ystad-Smyge-Ystad (6.5 h)	5201	30	15	36	156	-	-
12.4	Höllviksnäs-Skanör-Falsterborev-Abbekås-Höllviksnäs (11 h)	3728	48	11	833	107	6	-
12.4	Höllviksnäs-Barsebäck-Klagshamn-Falsterborev-Kämpinge	227	41	14	491	18	-	-
4.12	Kivik-Lägerholmen-Hanö-Åhus-Stenshuvud-Kivik (7 h)	7873	377	-	4	77	-	-
<u>1967</u>								
12.1	Skillinge-Smyge-Skillinge (7 h)	2581	121	-	9	150	29	-
9.2	Höllviksnäs-Falsterborev-Smyge-Trelleborg (7 h)	579	156	4	223	96	-	-
12.2	Ystad-Smyge-Sandhammaren-Ystad (8 h)	3733	693	-	7	453	-	-
28.3	Simrishamn-Lägerholmen-Åhus-Kivik (7 h)	1418	103	1	-	2	3	-



Table 6. The percentage distribution of the Tufted Duck, *Aythya fuligula*, in the sectors (Fig. 3) of the south coast study area in December-March 1964/65-1966/67 from the totals for the whole winter.

Sector	1964/65	1965/66	1966/67
A-B	22.5	36.2	16.6
D	+	3.0	-
E	-	-	-
F	1.4	4.2	+
G-H	6.8	11.0	+
K-P	+	+	+
R-S	37.8	17.0	61.6
T	17.3	15.5	1.5
U	1.3	2.5	+
V	8.6	10.6	20.3
X	4.3	+	+
Total numbers counted	2893	11450	4204

Table 7. The distribution of feeding Goldeneyes, *Bucephala clangula*, over various bottom types in Saltviken (A), Öresund, in December-March 1964-66 from accumulated totals of mappings in the study period. The distribution of the bottom types in the area can be seen from Fig. 2.

Bottom type	Depth (m)	Area (ha)	Total Found	per bottom type Expected	χ^2
Sand mixed with silt inside sandbanks	0-0.5	53	235	268	4
Sand with low vegetation outside sandbanks	0.4-1.0	51	361	254	45
Stony bottom near the shore	0.5-1.2	12	239	61	519
Zostera-meadows	1.0-6.0	126	373	625	102
Total		242	1208	1208	670



Table 8. The distribution of Goldeneyes, *Bucephala clangula*, off various shore-types (Fig. 3) in the area between Ystad and W. Hörte (A-H) in the south coast study area according to accumulated totals from mappings in the winter season (December-March) during the period January 1965 to March 1967. The numbers actually found are compared with the numbers expected if the Goldeneyes were distributed at random.

Shore-type	Length	Numbers observed			% Observed out of numbers expected		
		Indiv.	Flocks		Indiv.	Flocks	
			25-50	50-		25-50	50-
1. Marked moraine points with stony bottom outside	2.9	7277	51	33	264	327	416
2. Stony shores without marked points	3.5	3644	27	14	136	143	147
3. Stony walls near harbours stony bottom	1.3	862	5	1	87	72	28
4. Sandy shore, boulders in the water, stony bottom	8.0	4117	37	15	74	86	69
5. Sandy shore, bottom of coarse sand with some stones, few boulders above water-level	3.0	1956	7	2	85	43	25
6. Sandy beaches, no stones	5.1	332	1	0	9	4	0
Total χ^2 for difference between found and expected numbers ($P < 0.001$)		11520	116	104			

Table 9. The distribution of Goldeneyes, *Bucephala clangula*, off various shore types (Fig. 3) in the area between Skateholm and Trelleborg (K-S) in the south coast study area according to accumulated totals from mappings in the winter season (December-March) during the period January 1965 to March 1967. The numbers actually found are compared with the numbers expected if the Goldeneyes were distributed at random.

Shore-type	Length (km)	Total numbers		χ^2
		Counted	Expected	
3. Stony walls near harbours, stony bottom	1.6	499	175	599
4. Rubble stones, stony bottom	2.9	592	318	236
5. Sandy shore, boulders in the water, stony bottom	2.8	561	307	210
6. Sandy shore, bottom of coarse sand with some stones, few boulders above water-level	8.7	919	952	1
7. Sandy beaches, no stones	9.2	188	1007	666
Total	25.2	2759	2759	1712 ($P < 0.001$)



Table 10. The percentage distribution of Eider, *Somateria mollissima*, in various sectors (Fig. 2) of the Öresund study area in September-March 1965/66-1966/67 calculated from the accumulated totals in the respective winters.

Sector	1965/66	1966/67
A-C	13.0	16.5
D-E	1.9	2.8
G	2.3	0.7
H-L	37.3	21.9
N	17.1	29.5
P	3.5	3.3
R	18.0	21.2
S-U	6.9	4.1
Total numbers counted	521	461

Table 11. The distribution of Eider, *Somateria mollissima*, off various shore-types (Fig. 3) in the area between Ystad and W. Hörte (A-H) in the south coast study area according to accumulated totals from mappings in the winter season (December-March) during the period January 1965 to March 1967. The numbers actually found are compared with the numbers expected if the Eiders were distributed at random.

Shore-type	Length (km)	Total numbers Counted	Expected	χ^2
1. Marked moraine points with stony bottom outside	2.9	166	52	250
2. Stony shores without marked points, stony bottom	3.5	48	63	4
3. Stony walls near harbours stony bottom	1.3	91	24	187
5. Sandy shores, boulders in the water, stony bottom	8.0	77	145	32
6. Sandy shore, bottom of coarse sand with some stones, few boulders above water-level	3.0	20	54	21
7. Sandy beaches, no stones	5.1	28	92	45
Total	23.8	430	430	539 $P < 0.001$



Table 12. The distribution of Goosanders, Mergus merganser, off various shore types (Fig. 3) in the area between Ystad and W. Hörte (A-H) in the south coast study area according to accumulated totals from mappings in the winter season (December-March) during the period January 1965 to March 1967. The numbers actually found are compared with the numbers expected if the Goosanders were distributed at random.

Shore-type	Length (km)	Total numbers		χ^2
		Counted	Expected	
1. Marked moraine points with stony bottom outside	2.9	892	182	2770
2. Stony shores without marked points, stony bottom	3.5	164	220	14
3. Stony walls near harbours, stony bottom	1.3	189	82	139
5. Sandy shore, boulders in the water, stony bottom	8.0	187	503	199
6. Sandy shore, bottom of coarse sand with some stones, few boulders above water level	3.0	45	189	110
7. Sandy beaches, no stones	5.1	21	322	281
Total	23.8	1498	1498	3513 $P < 0.001$



Table 13. The percentage distribution of Goosander, Mergus merganser, in the sectors (Fig. 2) of the Öresund study area in September-March 1964/65-1966/67 calculated from the accumulated totals for the respective season. The Malmö harbour (M) was not counted in 1964/65 and is thus not included; the area had few Goosanders in the winter seasons studied.

Sector	1964/65	1965/66	1966/67
A	1.5	-	0.5
B	-	-	-
C	56.7	23.0	51.5
D	4.3	2.7	10.6
E	0.4	1.3	2.3
G	0.8	-	3.6
H-J	7.7	14.9	12.3
L	-	1.2	2.5
N	2.3	6.4	4.3
P	3.1	7.3	-
R	3.9	8.6	1.7
S	4.6	24.3	7.3
T	1.2	1.0	0.8
U	13.5	9.3	2.6
Total numbers counted	259	409	923



Table 14. The percentage distribution of Smew, Mergus albellus, in Lommabukten (A-K), Öresund, in November-March 1964/65-1966/67 calculated from the accumulated totals for the respective season.

Sector	1964/65	1965/66	1966/67
A	0.9	-	-
B	2.6	2.6	-
C	10.5	11.9	11.0
D	13.4	1.0	1.5
E	5.7	1.0	-
F	15.6	16.6	10.3
G	1.3	2.1	-
H	26.8	21.3	17.6
J	-	-	-
K	18.9	26.4	25.7
L	4.3	17.1	33.9
Total numbers counted	228	193	136



Table 15. The composition of the diet of the Tufted Ducks, Aythya fuligula, from the Bjärred area (D+E), Öresund, according to the oesophagus contents of specimens collected at Habo during the morning flight in 1966-1968. Numbers analysed shown in the heading under the respective month.

Food-item	Weight-%		
	September 8	December 4	March 2
Hydrobiidae spp.	54.8	13.1	77.8
Cardium lamarckii	41.0	33.0	1.8
Mytilus edulis	1.7	44.5	0.1
Macoma baltica	+	-	19.3
Mya arenaria	1.2	1.7	0.3
Gammarus sp.	0.7	1.7	-
Idothea sp.	0.2	0.7	-
Sphaeroma sp.	0.1	0.4	0.1
Corophium sp.	0.2	-	+
Nereis diversicolor	+	0.1	0.6
Balanus sp.	+	-	-
Litorina sp.	0.1	4.8	-
Theodoxus fluviatilis	+	+	-
Cyathura carinata	-	+	-
Total amount of food analysed (g)	177.3	17.5	19.3

Table 16. The composition of the diet of the Long-tailed Duck, Clangula hyemalis, according to the oesophagus contents (weight %) of specimens collected at Abbekås. Numbers of specimen showed in the heading.

Food-item	March (7)	December (3)
<i>Mytilus edulis</i>	95.8	27.2
<i>Macoma baltica</i>	0.5	—
<i>Litorina</i> sp.	1.1	—
<i>Gammarus</i> sp.	2.1	58.0
<i>Corophium</i> sp.	0.1	—
<i>Idothea baltica</i>	0.2	1.4
<i>Mysidacea</i> spp.	0.2	0.2
<i>Pleuronectes flesus</i>	—	13.2
Total amount of food in oesophagus analysed (g)	29.6	12.8

Table 17. Mean duration of dives and pauses together with mean dive/pause ratios for various depths in some species of diving ducks at the coasts of Scania. Mean values of the duration of dives and pauses were calculated from the means of the respective series.

Species	Depth (m)	Number of Ser.	Dive- pairs	Total Obs- time (min)	Duration of dive (secs.)			Duration of pause (sec.)		Dive/pause ratio	
					Mean	S.D.	Range	Mean	S.D.	Mean	S.D.
<i>Ardea marila</i>	0-1	1	10	4	12.9		9-20	12.8		1.0	
	1-2	1	11	5	15.9		9-23	10.3		1.5	
	3-4	1	6	4	26.7		25-29	17.3		1.5	
<i>Ardea fuligula</i>	0-1	6	82	27	13.6	4.6	3-21	7.9	2.8	1.9	0.8
	1-2	12	166	87	19.8	2.1	7-25	12.1	3.4	1.7	0.4
	2-3	16	199	105	20.2	2.5	13-27	12.0	2.5	1.8	0.4
	5-6	1	7	7	31.3		28-34	26.0		1.2	
<i>Ardea ferina</i>	0-1	1	24	9	15.1		13-19	7.6		2.0	
<i>Accephala clang.</i> ♂	0- $\frac{1}{2}$	1	21	3	6.6		4-9	2.8		2.4	
	$\frac{1}{2}$ -1	3	48	20	18.5	2.0	12-25	7.8	1.8	2.5	0.5
	1-2	17	232	117	21.0	2.9	12-33	8.6	1.9	2.5	0.5
	2-3	15	243	132	22.9	2.1	12-30	9.3	1.7	2.6	0.4
	3-4	2	25	17	27.2		24-33	12.2		2.1	
	4-5	1	7	5	28.6		25-31	10.1		2.8	
<i>Accephala clang.</i> ♀	0- $\frac{1}{2}$	8	169	35	8.8	1.1	2-18	3.6	0.8	2.6	0.8
	$\frac{1}{2}$ -1	9	183	62	15.4	1.5	5-20	5.2	0.8	2.9	0.5
	1-2	12	199	90	20.4	2.8	12-34	7.2	1.6	2.9	0.7
	2-3	11	182	100	23.4	2.5	15-33	9.5	2.9	2.6	0.7
	3-4	2	26	16	26.1		23-28	11.1		2.5	
	4-5	3	34	21	28.3	0.5	24-31	9.9	0.7	2.9	0.3
<i>Angula hyemalis</i>	0-1	8	122	41	15.3	2.8	5-23	3.9	1.0	3.7	0.9
	1-2	14	176	90	24.2	5.1	13-37	6.8	2.6	3.8	0.9
	2-3	7	144	73	30.2	4.5	19-40	9.2	1.4	3.4	1.0
	3-4	1	25	22	38.4		35-42	13.2		2.9	
	4-5	7	75	41	38.3	3.6	31-45	10.1	1.2	3.9	0.8
	6-7	11	95	100	46.4	2.5	37-51	17.0	1.6	2.8	0.2
<i>Amatoria mollissima</i>	2-3	5	74	65	31.2	12.7	9-59	26.5	9.7	1.3	0.5
<i>Argus merganser</i>	1-2	4	54	26	20.3	2.3	11-31	10.2	4.3	2.3	0.7
	2-3	4	51	29	23.5	3.9	11-32	10.9	2.0	2.2	0.6
	4-5	2	24	17	27.5		21-34	11.5		2.6	
<i>Argus albellus</i>	1-2	10	114	50	18.2	2.3	8-26	8.2	1.5	2.4	0.3

Table 18. The exploitation of the bottom fauna of different sectors of the Öresund study area by diving ducks. Bird-day units were calculated from counts made almost once a week. For sector D-E only the area out to a depth of 3 m is considered.

Sector	Area (ha)	Season	Number of bird-day units (Sept.-April)					Total	Mean consumption g/m ² with a con- sumption of 200 g/bird/day
			Aythya marila	Aythya fulig.	Aythya ferina	Bucep. clang.	Somat. moll.		
	310	64-65	-	300	-	9600	100	10,000	0.6
		65-66	-	1100	-	17600	800	19,500	1.3
		66-67	-	-	-	19900	400	20,300	1.3
	160	64-65	-	700	-	10900	1000	12,600	1.6
		65-66	200	18900	-	23800	1400	44,300	5.5
		66-67	-	-	-	21800	1800	23,600	2.9
D-E	(410)	64-65	16600	127000	-	44700	300	188,600	9.2
		65-66	21200	91000	-	101000	200	213,400	10.4
		66-67	15400	88400	-	74200	100	178,100	8.7
D-L	1090	64-65	22200	135000	10900	16400	(800?)	185,300	3.4
		65-66	11100	248000	5900	34400	8100	307,500	5.6
		66-67	7900	292000	5700	33800	3100	342,500	6.3
	330	65-66	100	446000	-	37800	3000	486,900	29.4
		66-67	400	344000	-	38900	4000	387,300	23.4
	660	64-65	100	2400	-	2300	200	5,000	0.2
		65-66	-	3000	-	4600	1100	8,700	0.3
		66-67	-	400	-	3100	400	3,900	0.1
D-S	4090	65-66	42500	976000	6100	220000	15700	1,260,300	6.2
		66-67	25000	741000	6000	205000	19200	996,200	4.9

Table 19. Standing crop (g/m^2 fresh weight in 80 % alcohol) of some important food items in three sectors of the Öresund study area in April 1966. Mean values $\pm$ standard deviation. + = patchy distribution

Sector	Bottom type (See Fig.2)	No of samples	Mytilus	Cardium	Gammarus	Idothea	Nereis
A	Zostera (3)	7	184 $\pm$ 47	+	2.4 $\pm$ 0.8	1.7 $\pm$ 0.6	0.9 $\pm$ 0.4
	Sand&silt (2)	15	+	+	+	+	12.9 $\pm$ 02.0
D-E	Zostera (3)	13	311 $\pm$ 90	+	5.4 $\pm$ 1.3	1.6 $\pm$ 0.4	2.8 $\pm$ 0.7
	Mud (1)	44	+	14.6 $\pm$ 3.5	2.8 $\pm$ 0.4	+	27.5 $\pm$ 4.2
S	Zostera (3)	10	141 $\pm$ 55	10.8 $\pm$ 3.0	8.2 $\pm$ 2.0	0.9 $\pm$ 0.6	+
	Sand&silt (2)	8	+	63.5 $\pm$ 18.3	3.1 $\pm$ 0.9	+	11.6 $\pm$ 3.4

Table 20. The exploitation of the bottom fauna of different sectors of the south coast study area by diving ducks.

Sector	Area (ha)	Season	Number of bird-day units (Oct.-April)					Total	Mean consumption g/m^2 with a con- sumption of 200 g/bird/day
			Aythya marila	Aythya fulig.	Bucep. clang.	Clang. hyema.	Som. moll.		
A-B	300	64-65	-	11200	29800	32900	1200	75,100	5.0
		65-66	100	34900	62500	63000	1700	162,200	10.8
		66-67	-	9400	57400	62500	100	129,400	8.6
G-H	220	64-65	-	1500	58600	44200	1500	105,800	9.5
		65-66	-	10200	65100	73500	2100	150,900	13.7
		66-67	-	-	50000	33800	100	83,900	7.6
U-X	430	64-65	-	4100	11300	1600	1100	18,100	0.8
		65-66	-	8700	13000	2400	2900	27,000	1.3
		66-67	600	12600	10400	200	500	24,300	1.1
Whole area (A-X)	3190	64-65	-	44700	159000	108000	6400	318,100	2.0
		65-66	700	107000	225000	232000	15000	579,700	3.6
		66-67	600	63000	193000	153000	2900	412,500	2.6



Fig.1. Map of southernmost Sweden showing the general position of the study areas.



- | | |
|---|---|
|  | 1 Muddy bottom |
|  | 2 Sand mixed with silt |
|  | 3 Vegetation free sand |
|  | 4 <i>Zostera</i> -zone |
|  | 5 Natural stony bottom |
|  | 6 Stony bottom, mainly material dumped in the Malmö harbour area, some natural bottom |

Fig. 2. Map of the Öresund study area showing the division into sectors (A-V) and bottom types out to a depth of 6 m. The depth curve for 3 m is shown in Fig. 10.

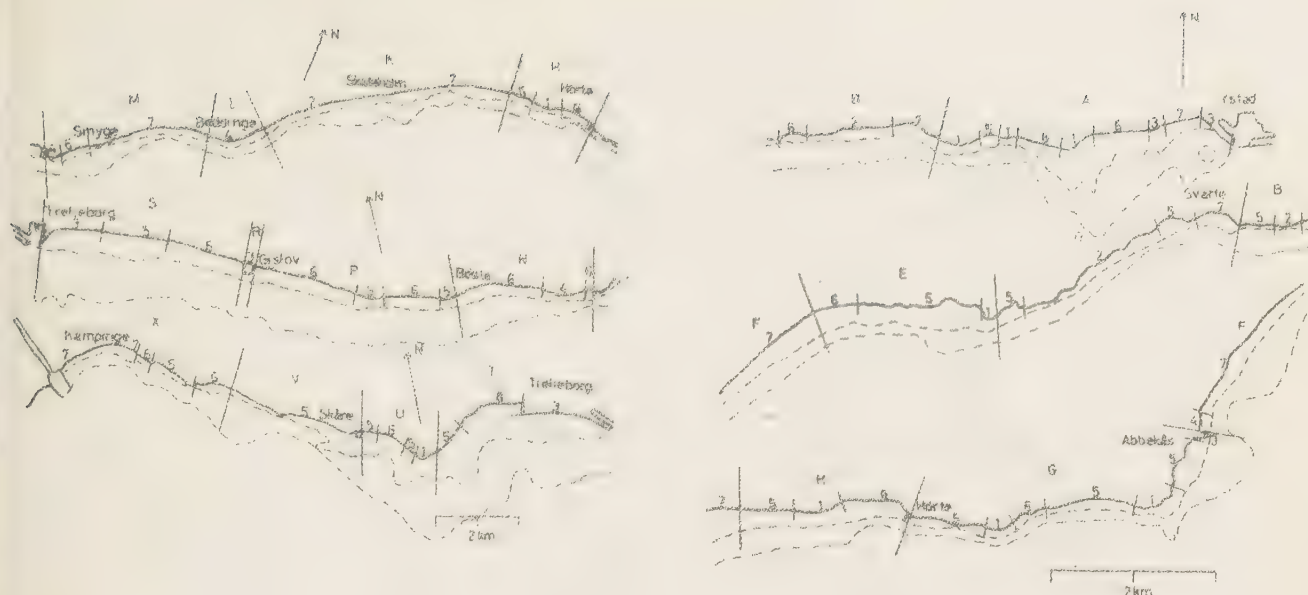


Fig.3. Map showing the south coast study area with divisions into sectors (A-X) from east to west, the depth curves for 3 and 6 m and the division into different shore-types (1-8):

- 1) marked moraine points with large boulders appearing above water-level and bottom almost covered with stones of varying sizes.
- 2) stony shore with large boulders above water-level but without marked points.
- 3) stony walls near harbours with stony bottom outside.
- 4) rubble-stones.
- 5) sandy shore with large boulders above water-level just outside and stony bottom except near the shore.
- 6) sandy shore with few large boulders above water-level and bottom with coarse sand and gravel and only few stones.
- 7) sandy beaches with sandy bottom to about 300-500 m from the shore, where it grades into stony bottom.
- 8) stony bottom with mud in shallow water (below 1 m) water that grades into stony bottom in deeper water about 500 m from the shore.



Fig.4. Map showing the Sölvesborg study area.

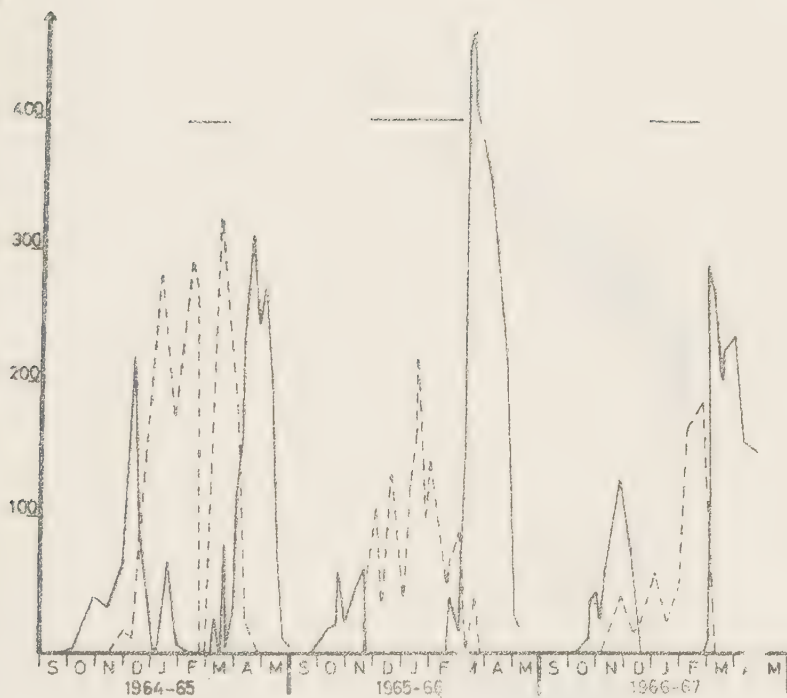


Fig.5. Number of Scaups, *Aythya marila*, counted at Habo (F) (whole line) and Sjölund (H) (broken line) in the Öresund area in 1964/65-1966/67. Horizontal lines show the period when the ponds at Habo were covered with ice.



Fig. 6. The direction of feeding flights of Tufted Ducks, *Aythya fuligula*, from daytime resting places (R) in the northern parts of the Öresund study area. The hatched area was used as a resting place when the ponds at Habo (F) were frozen in spring. Circles show places where feeding Tufted Ducks were seen at night or found dead in nets. The marked area is enlarged in Fig. 7.

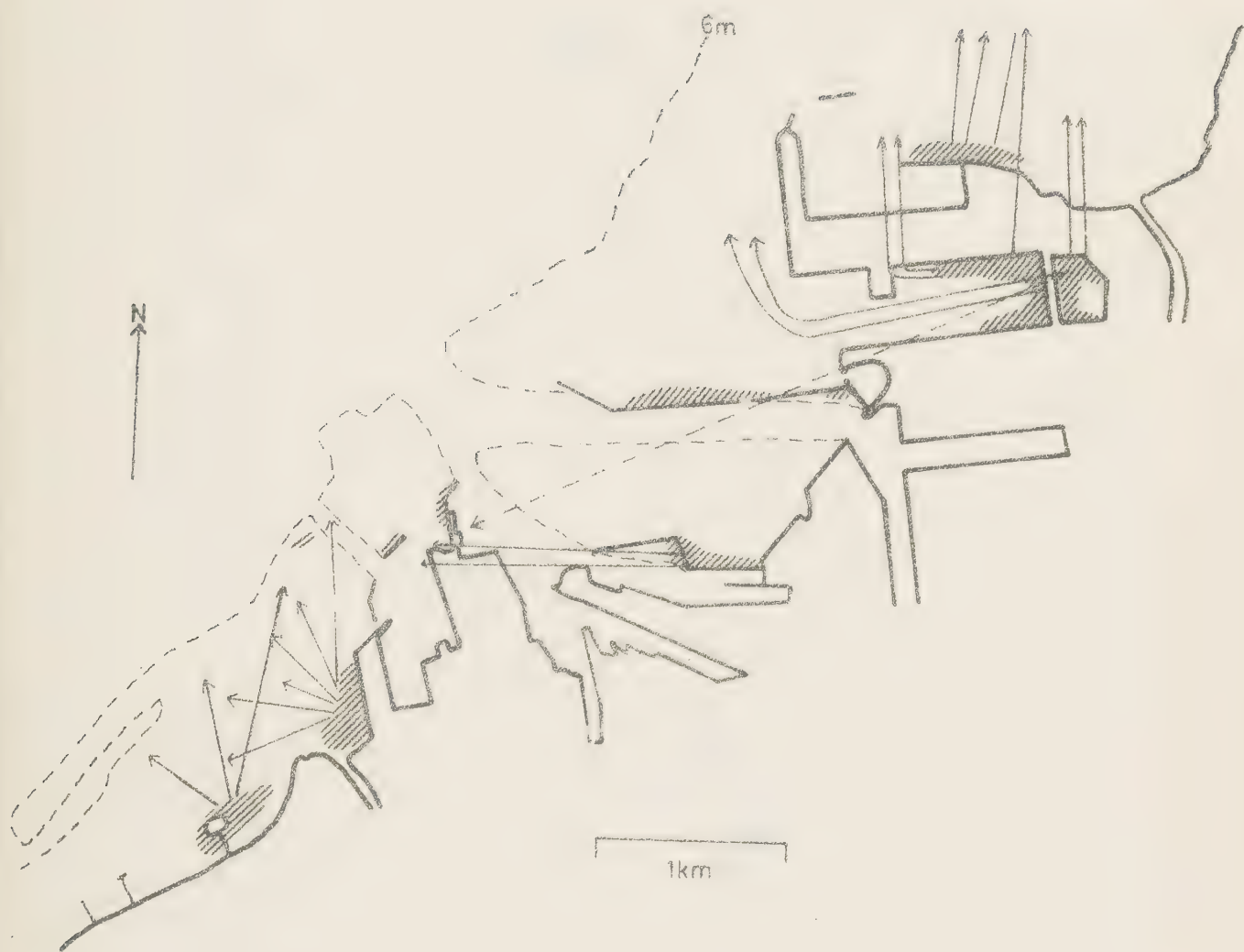


Fig.7. Daytime resting places (hatched areas) and the directions of feeding flights (arrows) for Tufted Ducks, *Aythya fuligula*, in the Malmö harbour area. The outer areas were only used as resting places when the innermost ones were frozen.



Fig.8. The direction of feeding flights from daytime resting places(R) of Tufted Ducks, Aythya fuligula, in the Klagshamn-Falsterbo area.
x = stony shoals.

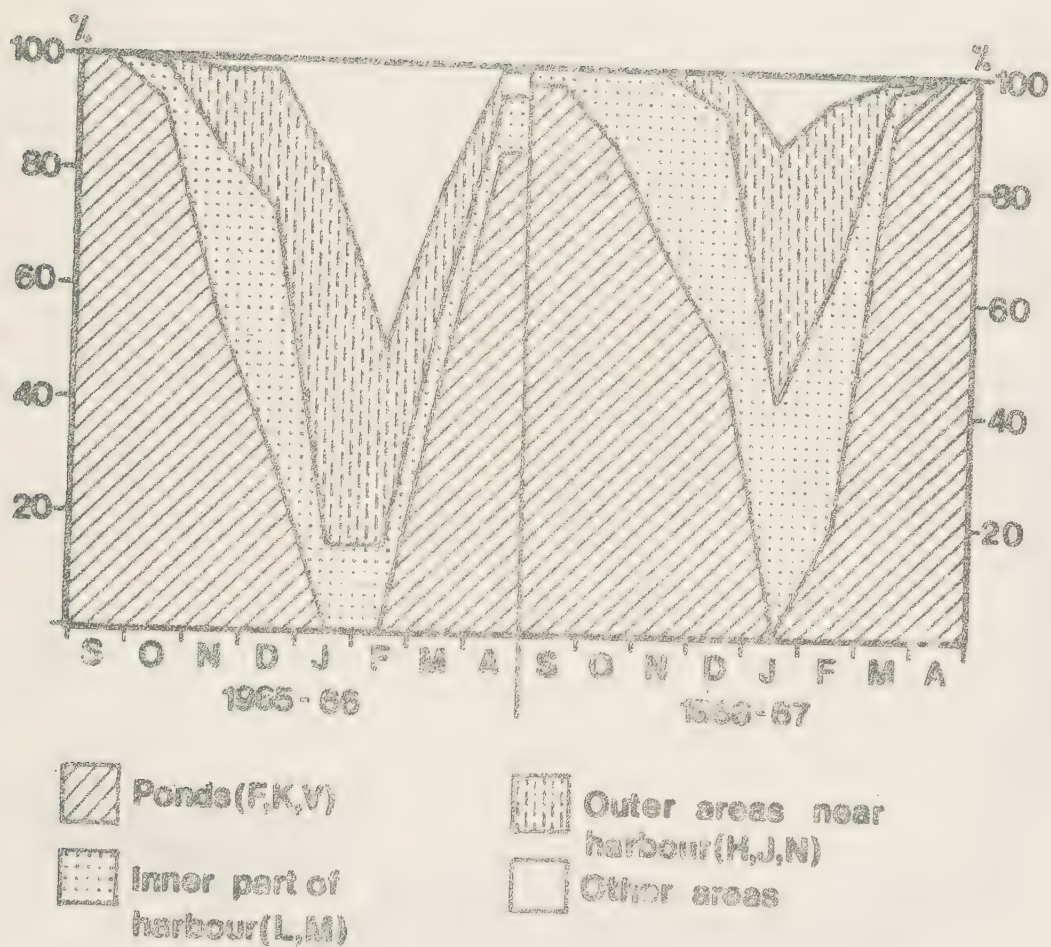


Fig. 9. The distribution of Tufted Ducks, *Aythya fuligula*, in different types of habitats in the Öresund study area in 1965/66 and 1966/67 based on monthly means.



Fig.10. Map showing the daytime feeding areas (hatched and points) and nighttime resting places (cross-hatched) of the Goldeneye, Bucephala clangula, in parts of the Öresund area. Feeding areas marked with points were used only by a few individuals or when the shallow areas were frozen. The curves for 3 m and 6 m depth are also shown (broken lines).

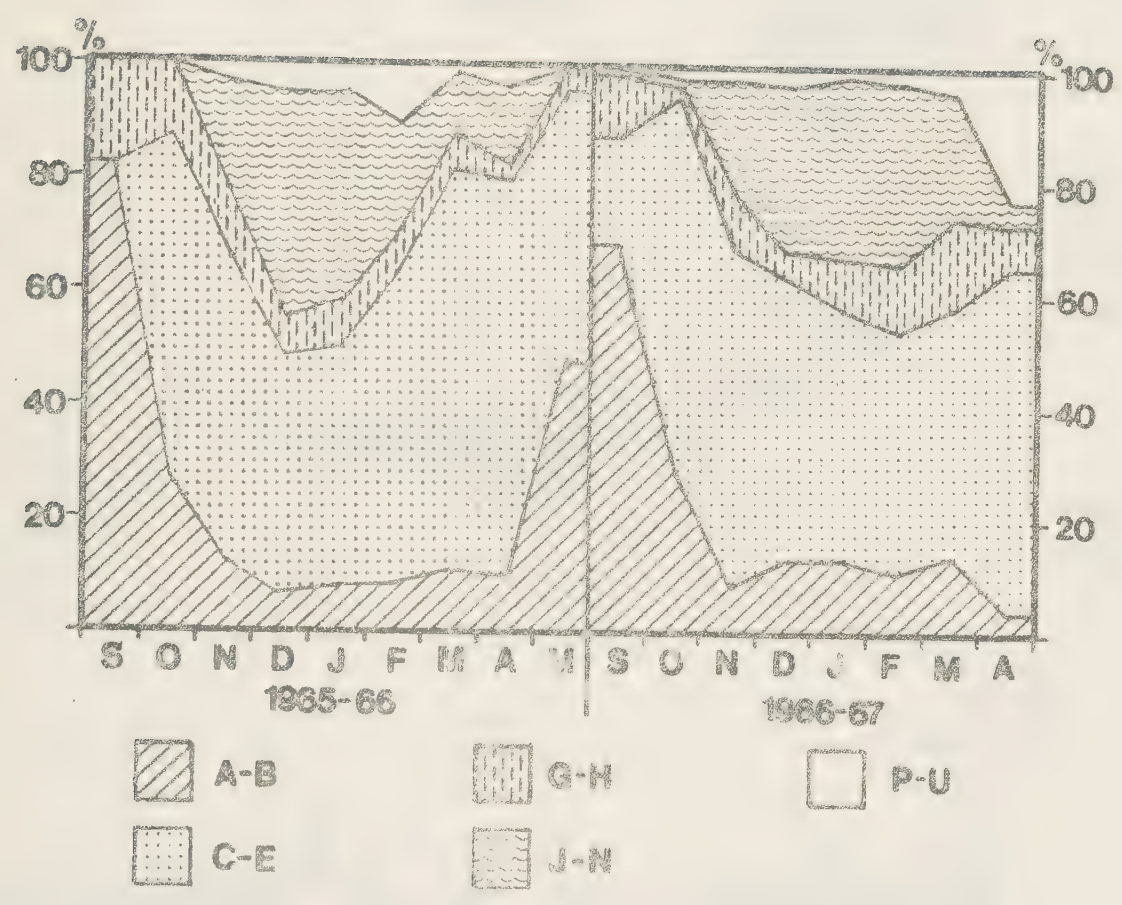


Fig.11. The distribution of Goldeneyes, *Bucephala clangula*, in different parts of the Öresund study area during the winters 1965/66 and 1966/67 based on monthly means.

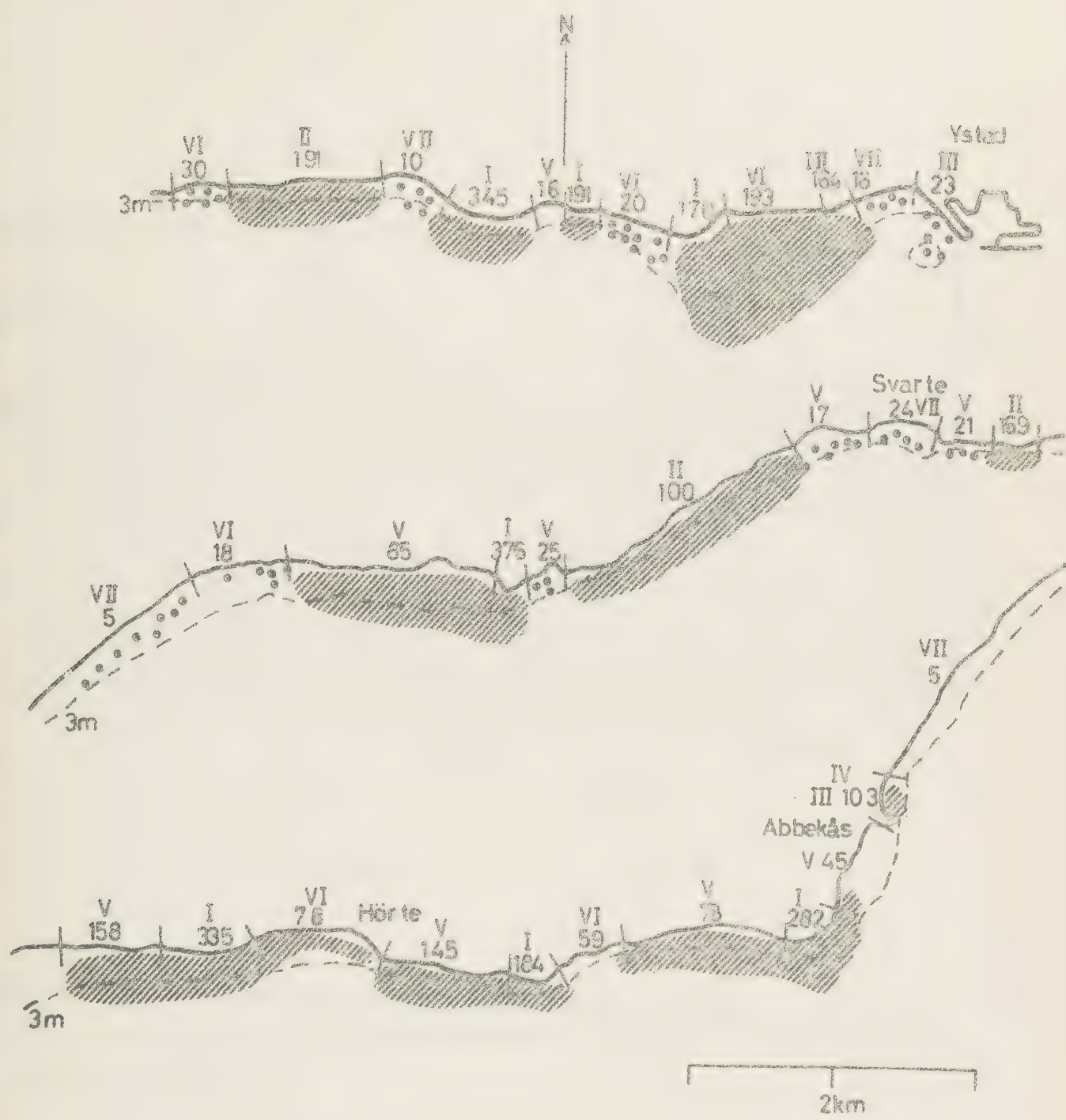


Fig.12. Map showing the distribution of the daytime feeding areas (hatched and dots) of the Goldeneye, *Bucephala clangula*, in parts of the south coast study area. The shore line is divided into sectors according to the shore type (Roman numerals-for explanation see Fig.3!). The (arabic) figure for each shore type is the number of Goldeneyes seen in the sector as per cent of the number expected if the Goldeneyes were distributed at random over all bottom types.

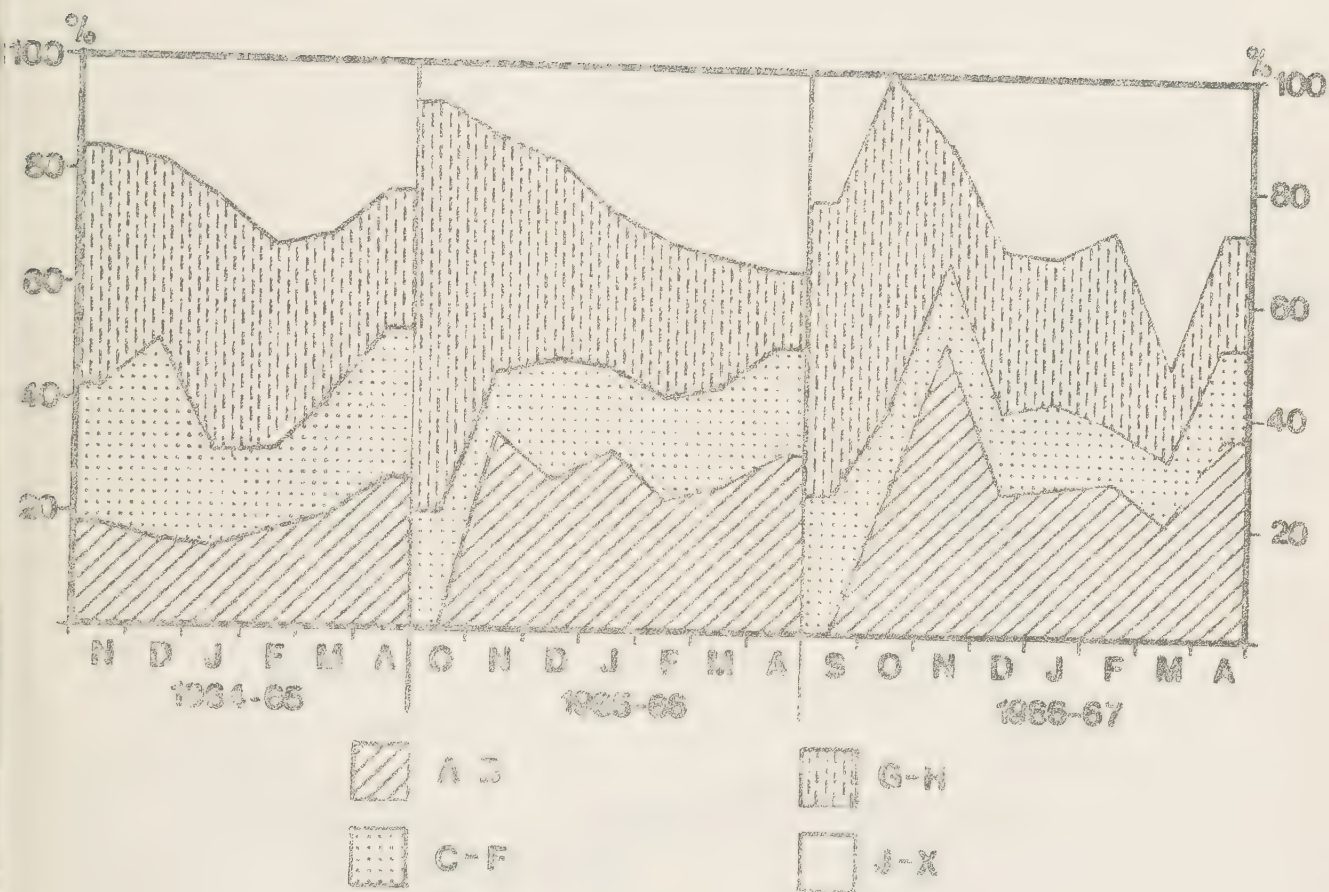


Fig.13. The distribution of Goldeneyes, *Bucephala clangula*, in different sectors of the south coast study area during the winters 1964/65-1966/67 based on monthly means.



Fig.14. The daytime distribution of the Long-tailed Puck, Clangula hyemalis, on the coasts of Scania. Hatched = areas with more than 100 individuals observed per 1 km survey line, dotted = areas with more than 25 individuals per 1 km survey line. The survey lines are marked with fine lines on the map and the 20 m depth curve with a broken line. No Long-tailed Ducks were found outside the whole lines crossing the survey lines.

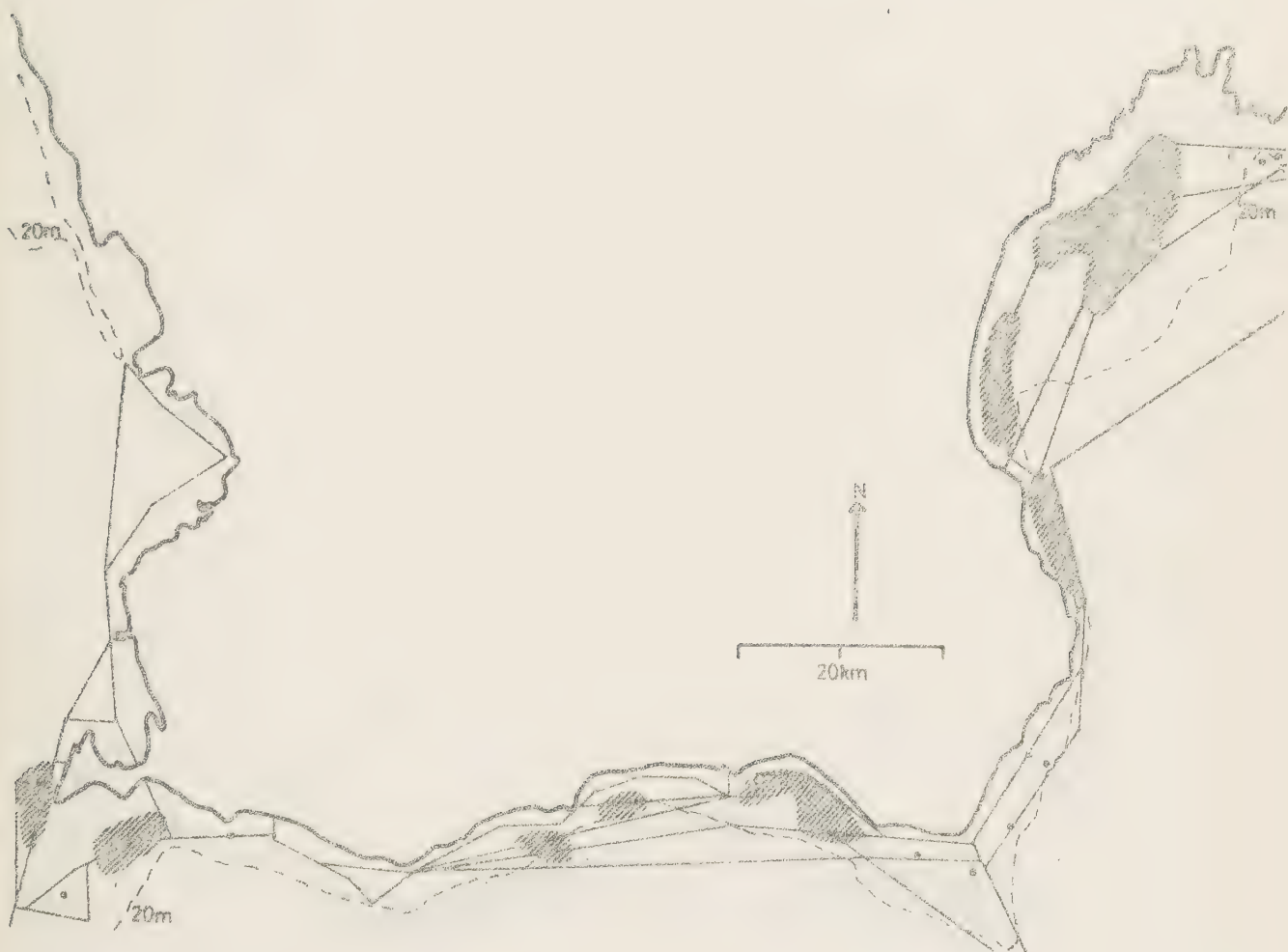


Fig.15. The daytime distribution of the Velvet Scoter, *Melanitta fusca*, on the coasts of Scania. Hatched = areas where flocks were observed regularly, dots = single observations. The 20 m depth curve (broken line) and the survey lines are also shown on the map.



Fig.16. The daytime distribution of the Red-breasted Merganser, Mergus serrator, on the coasts of Scania. Hatched = areas where flocks and single individuals were regularly seen during the surveys at sea, dots = single observations. The 20 m depth curve (broken line) and the survey lines are also shown on the map.

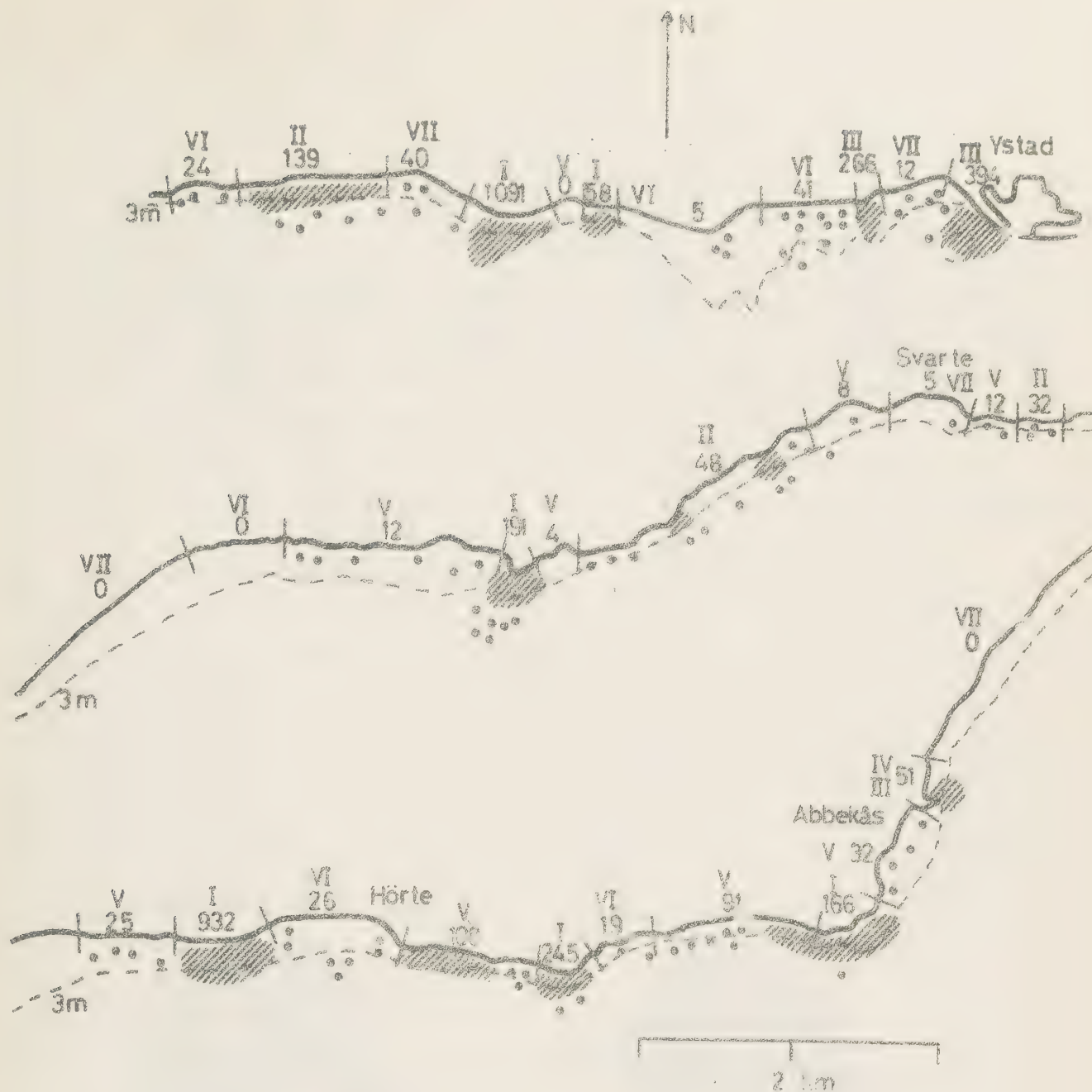
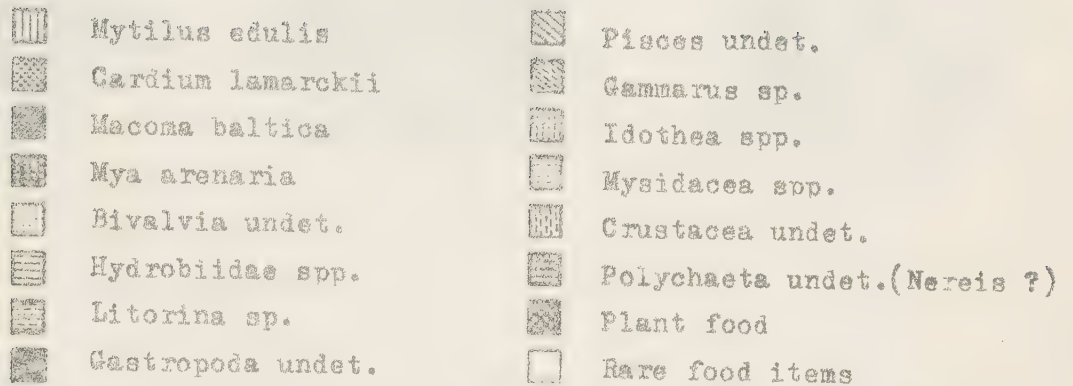
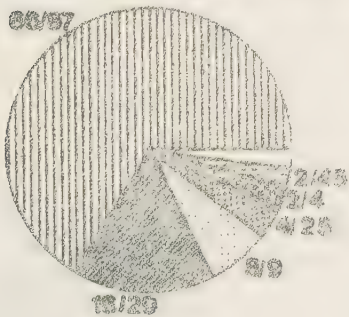


Fig.17. The daytime distribution of the Goosander, *Mergus merganser*, in parts of the south coast study area. Hatched = areas of regular occurrence, dots = areas more seldom used. The shore line is divided into sectors according to the shore type (Roman numerals - for explanation see Fig.3!). The (arabic) figure for each shore-type is the number of Goosanders seen in the sector as per cent of the number expected if the Goosanders were distributed at random over all bottom types.



Key to Figs. 18-23.

Habo March-April 67-68/24



Sölvesborg Dec. 66-73 (6)

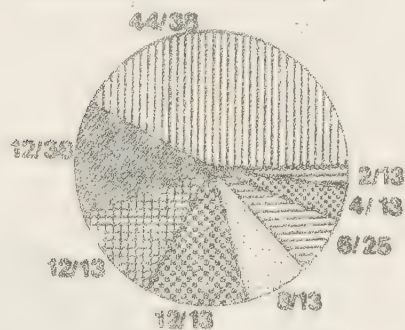


Fig. 18. The composition of the diet of Scaups, *Aythya marila*. The width of the sectors and the first figure denote the percentage of each major food item according to the estimation method and the second figure for each sector the frequency of occurrence of the item. Number of stomachs analysed in brackets.

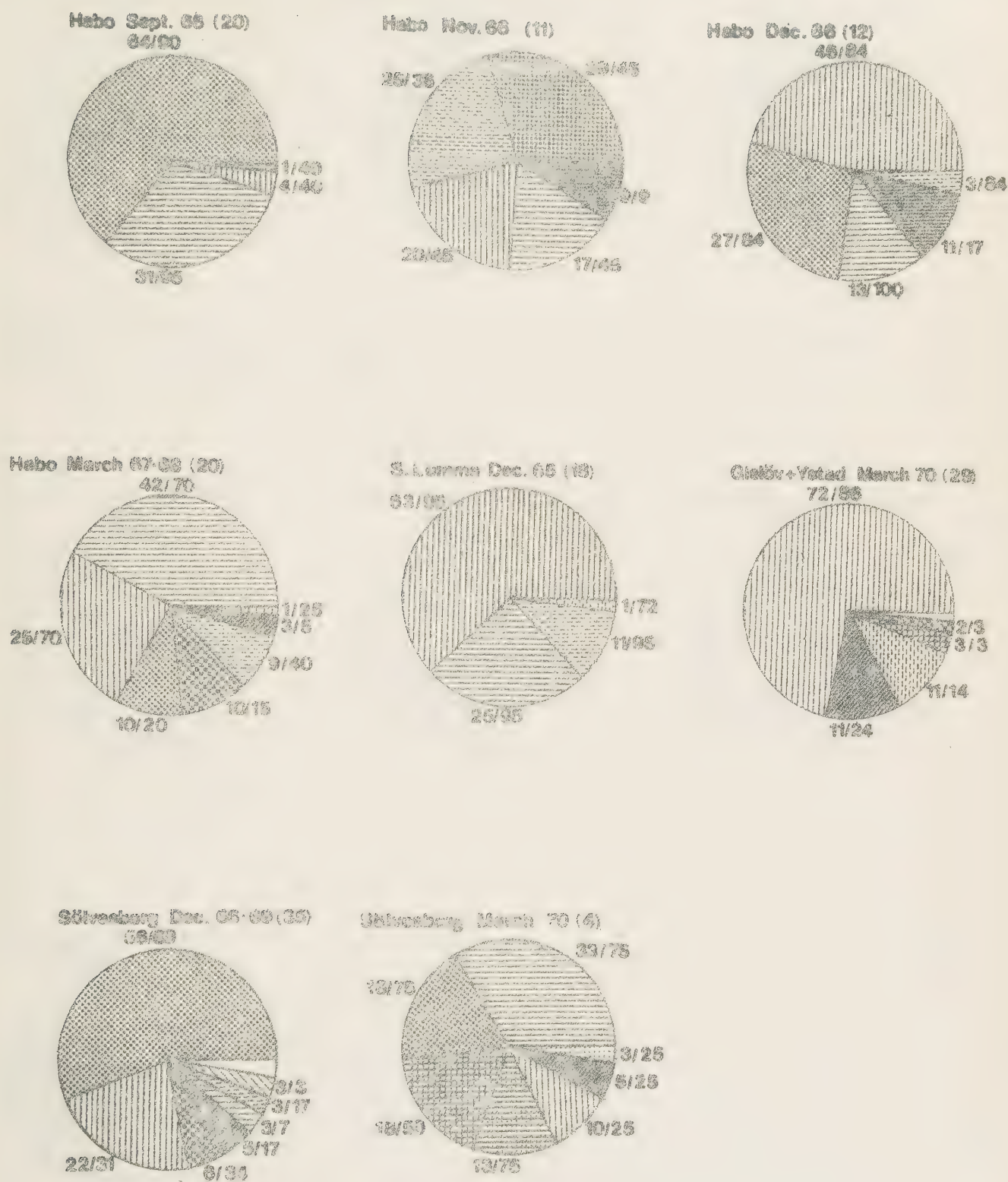
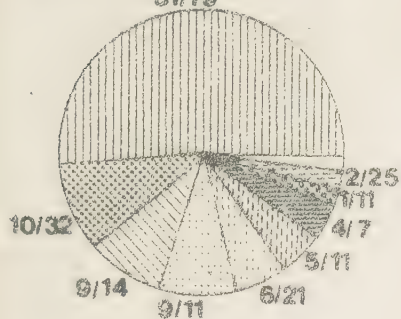


Fig. 19. The composition of the diet of Tufted Ducks, *Aythya fuligula*.
For further explanation see Fig. 16!

Sölvesborg Dec. 66-69 (28)
51/79

Sölvesborg March-April 70 (21)

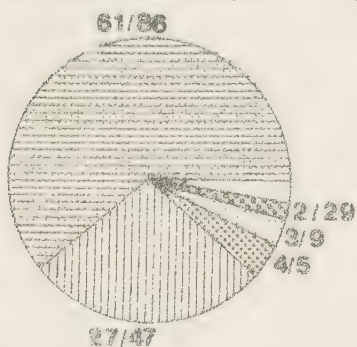
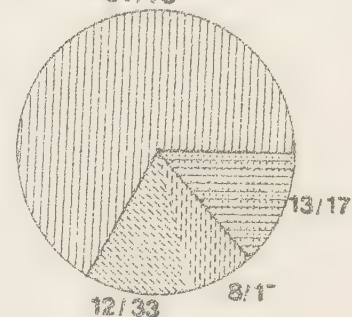
Ystad March 70 (12)
67/75

Fig.20. The composition of the diet of Goldeneyes, Bucephala clangula.
For further explanation see Fig.18!

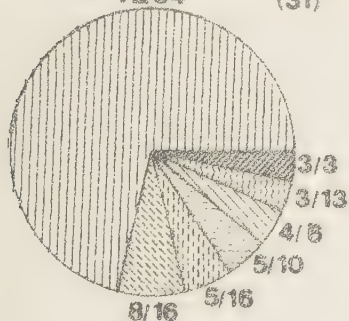
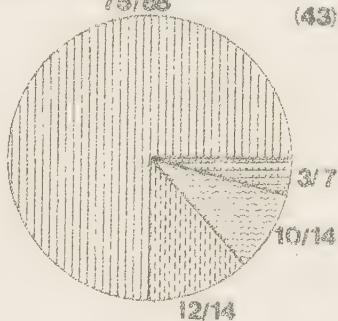
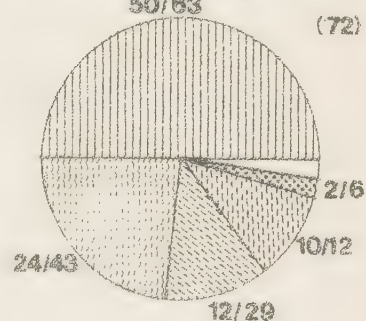
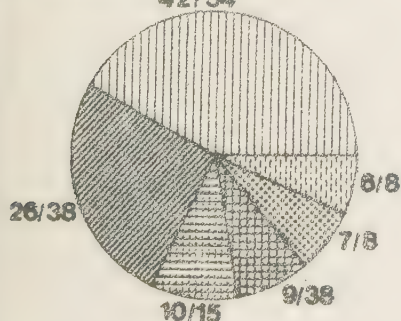
Abbekås+Ystad Dec. 66-69
72/84 (31)Abbekås+Ystad March 66-70
75/88 (43)Sölvesborg Nov.-Dec. 66-69
50/63 (72)Sölvesborg April 70 (13)
42/54

Fig.21. The composition of the diet of Long-tailed Ducks, Clangula hyemalis.
For further explanation see Fig.18!

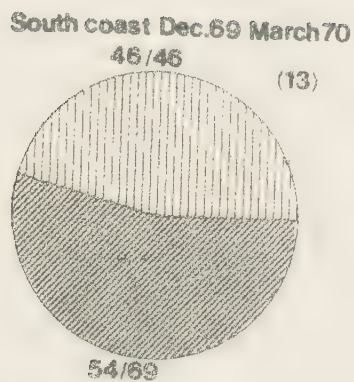


Fig.22. The composition of the diet of Common Scoters, Melanitta nigra.
For further explanation see Fig.18!

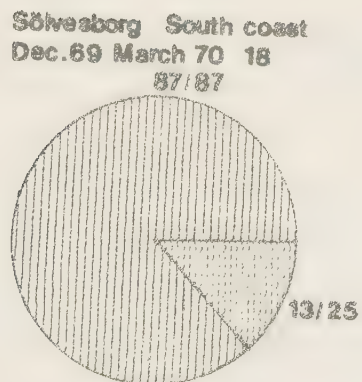


Fig.23. The composition of the diet of Eiders, Somateria mollissima.
For further explanation see Fig.18!

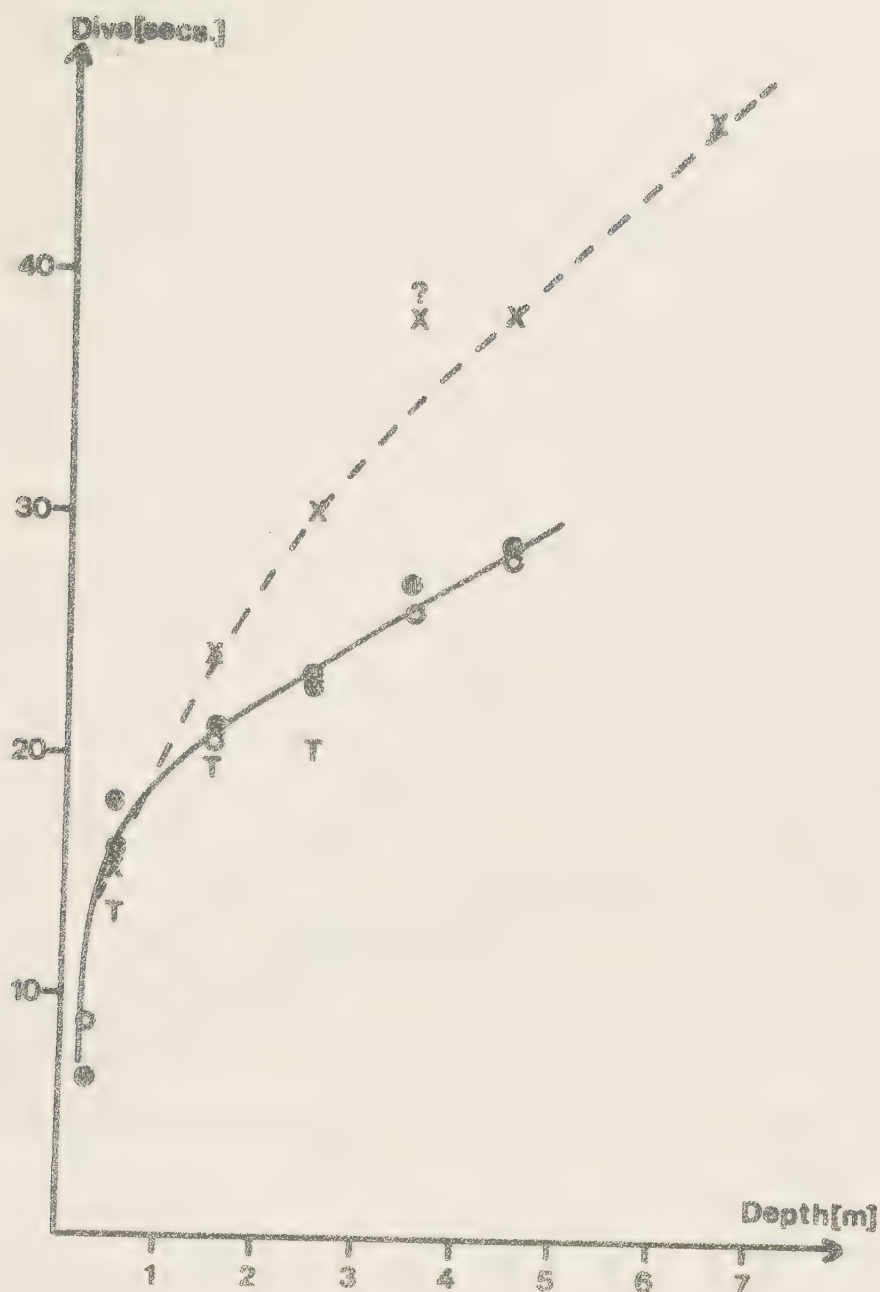


Fig.24. The relation between diving-time and depth for Tufted Duck, *Aythya fuligula*, (T), Goldeneye, *Bucephala clangula*, (—) and Long-tailed Duck, *Clangula hyemalis*, (---) at the coasts of south Sweden. Dives in depths less than 1 m were over muddy bottom, the other over stony bottom.

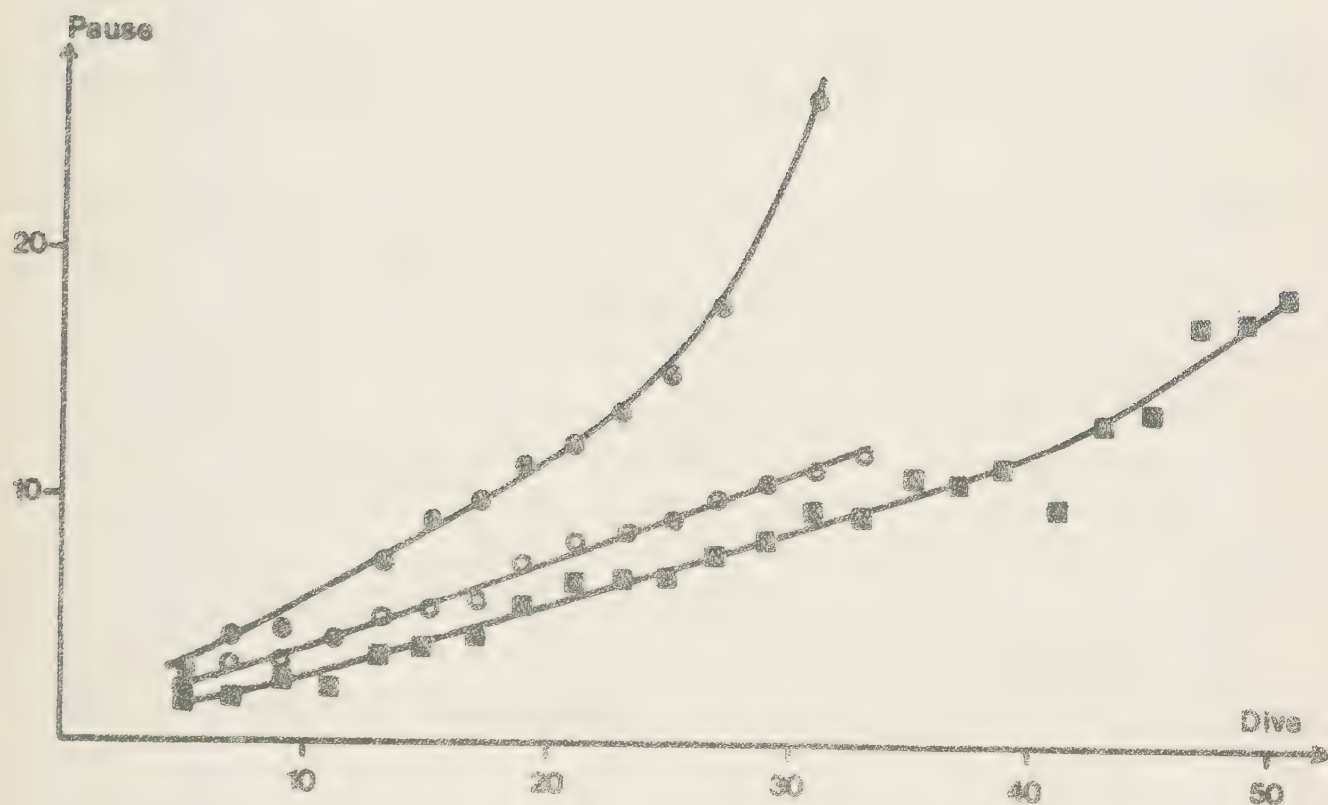


Fig.25. The relation between the pause between two dives and the length of the preceeding dive for Tufted Duck, Aythya fuligula, (filled circles), Goldeneye, Bucephala clangula, (open circles) and Long-tailed Duck, Clangula hyemalis, (filled squares). Means of all values obtained grouped according to diving time.

Habitat selection, food choice and food consumption of diving ducks on a south Swedish lake

Abstract

Lake Ringsjön in central Scania was used in summer as a moulting place for numerous Aythya fuligula and some Bucephala clangula and as resting place for these species as well as A. ferina and Mergus merganser and single individuals of other species during spring and autumn. M. merganser occurred all over the lake, whereas the other, bottom-feeding species were concentrated to parts of the lake. B. clangula was commonest in the most productive areas, whereas the night-active A. fuligula fed all over the lake.

A. fuligula had a diet markedly dominated by chironomid larvae and Pisidium spp., which together with oligochaetes dominated the macrofauna of the bottoms in the lake. B. clangula mainly fed on larvae of chironomids and Trichoptera. A. ferina took seeds and chironomid larvae.

From early August till late November the west lake was exploited by 125,800 bird-day units. With a consumption of 200 g per day this represents a total consumption of about 26 metric tons compared to a total standing crop in September of about 82 tons. The production of food species during the autumn was good and the standing crops of total food species and chironomid larva larvae increased, whereas Pisidium spp., a preferred food item of A. fuligula, decreased.

1. Introduction

The food choice of diving ducks in freshwater localities has been studied for a few species (cf. Cottam 1939, Madsen 1954, Olney 1963, 1968, Olney & Mills 1963 and papers cited in Bauer & Blotzheim 1969), but only one paper discusses habitat selection and feeding habits of European diving ducks on a freshwater locality in any detail (Sziij 1965). The food choice and food consumption in relation to the available food resources at a freshwater locality has not been investigated, whereas such studies have been published for marine localities (Geramisova & Baranova 1960, Nilsson 1969).

The purpose of the present study was to compare the distribution of the diving ducks with the distribution of the food species on a south Swedish lake and to compare the food intake of the ducks with the composition of the bottom fauna and the amount of available food. The field work of this

study was performed during March-May and August-November 1969 with some observations being made in 1968 and 1970.

2. Study area

The study was carried out on Lake Ringsjön in central Scania, south Sweden (Fig. 1). Lake Ringsjön consists of two lakes connected by a narrow channel about 200 m long, the main work being done in the west lake. It is situated in a hilly landscape and is bordered by deciduous forests, meadows and arable land. The lake is mesotrophic. The maximum depth of the west lake is 5 m and of the east lake 14 m. The bottom is mainly sandy near the shores with mud at depths greater than 2 m (Fig. 2). In some areas the sand has been covered with mud in recent years. Especially in sectors F and K the inner parts have a bottom substrate of very fine sand. In small areas the bottom consists of clay with mollusc shells.

Emergent vegetation occurred in a narrow belt along parts of the shores and consisted mainly of Phragmites communis Trin. with some Scirpus lacustris L.. The shores are mainly stony except for the main parts of sectors F and K and parts of sector G.

Earlier the lakes had a heavy growth of submerged vegetation, mainly Potamogeton spp. and Ceratophyllum demersum L. but most of this vegetation had disappeared before 1969. The west lake was intensively surveyed in August-November 1969, but only very small areas were covered with Ceratophyllum demersum, Potamogeton natans L. and smaller Potamogeton-species, most parts of the lake being free of vegetation. The vegetation was somewhat richer in sector G of the east lake. Areas with fine sand and a depth of less than 1 m, mainly in sectors F and K, had a carpet of Chara spp.. Other aquatic plants found in the lakes include Polygonum amphibium L. and Elodea canadensis Mich..

3. Methods

The composition of the bottom fauna was studied in the west lake and only a few samples were taken in the east lake for comparison. Quantitative samples were taken at 89 stations scattered over the west lake during the period September 4-9 (Figs. 3 and 4). At 11 stations in sector F 10 samples per station were taken whereas 3 samples per station were taken on each of the other stations. The stations in sector F were also sampled on 22 October and 25 November and 8 stations in sectors C and D were also sampled on 22 November. In October and November, 10 samples were in general taken per station. A Birge-Ekman grab (mounted on a handle) that sampled

0.017 m² was used. A sieve with 1 mm meshes was used and the material left on the sieve was preserved in 80 % alcohol and later sorted in the laboratory. Before weighing the specimens were dried between filter papers.

4 Scaups, Aythya marila (L.), 83 Tufted Ducks, Aythya fuligula (L.), 8 Pochards, Aythya ferina (L.), 19 Goldeneyes, Bucephala clangula (L.), 1 Long-tailed Duck, Clangula hyemalis (L.) and 1 Smew, Mergus albellus L. were obtained for stomach analysis from fishermen who caught them in the nets.

The gizzard and the oesophagus of the collected birds were removed and preserved in 80 % alcohol and their contents analysed separately. The oesophagus contents were sorted to species and counted. The gizzard contents were identified to species as far as possible and the proportions of the various food items were estimated in tenths of the total gizzard content. From these estimates the percentage composition of the diet was calculated. The reliability of the method will be discussed elsewhere (Nilsson in prep.).

Counts of the resting diving ducks on the lakes were made every week in the west lake and twice a month in the east lake on the same days as in the west lake. The counts started when the lakes became free of ice in late March 1969 and continued to May and were started again in early August and continued till late November when the lake was ice-covered. The position and the activity of the flocks were mapped during the counts except at times in spring when disturbing small boats made mapping impossible.

The weekly counts in the west lake served as a base for calculations of the use made of the area by the diving ducks in terms of bird-day units.

4. The bottom fauna of the west lake

As the ducks almost exclusively feed on the open water little attention was given to the fauna of the emergent vegetation. Various insect larvae were common here, especially larvae of Trichoptera, e.g. species of Limnephilus and Phryganea. The shore vegetation also contained various species of aquatic Hemiptera and Coleoptera and larvae of Odonata. Among the molluscs the following species were abundant: Limnaea stagnalis (L.), Tropidiscus planorbis (L.), Planorbis corneus (L.), Spirulina vortex (L.), Valvata cristata Müller and Gyraulus sp.. Various species of Hirudinea were common.

The bottom fauna was richest on the sand with or without Chara spp. and

was dominated by chironomid larvae, oligochaetes and Pisidium spp. (Tables 1-3). In September, maximum numbers of chironomid larvae were 11,000 per m², for oligochaetes over 10,000 and for Pisidium spp. about 4,500. It should be noted that small specimens of oligochaetes and chironomids pass the sieve. When comparing the standing crop of these items in various sectors of the lake in September different items dominated in the different sectors (Table 1). The maximum standing crop for one station was 24 g/m² of chironomid larvae and 42 g/m² for all items together (Figs. 3 and 4). The highest standing crops were noted at some stations close to the shore.

In sector F the composition of the fauna in the inner part with Chara spp. and the outer part without Chara spp. was similar but the proportions of the items were different (Tables 1 and 2).

Species found on the sand in smaller numbers were various Hirudinea, Sphaerium corneum (L.), Bithynia tentaculata (L.), Valvata cristata, Gammarus lacustris (L.), Asellus aquaticus (L.) (at a few stations with detritus), larvae of Molanna angustata Curtis and some other Trichoptera, larvae of Ephemeroptera and larvae of Sialis lutaria (L.).

The bottom fauna of the clay was sparser with mostly the same items as the sandy bottom but with a much lower standing crop (Table 1). Typical species of the sandy bottom such as Molanna were not found here.

The bottom fauna of the mud was sparser than that of the other bottom types and was largely dominated by chironomid larvae of the larger plumosus-type. The numbers of chironomid larvae were low, generally between 100 and 500 per m². Besides the chironomid larvae some oligochaetes and a few Hirudinea and some larvae of Sialis lutaria were obtained in the grabs.

Only small changes occurred in the standing crop during the autumn. In sector F there was an increase on the outer sandy bottom from September to October whereas the standing crop on the inner area decreased slightly during the same period (Table 2). The standing crop of chironomid larvae increased from September to October in both areas, whereas oligochaetes increased in the outer and decreased in the inner. A marked decrease in Pisidium spp. was found in the inner part. Between 22 October and 25 November only insignificant changes occurred.

In the west part of the lake a marked increase in the standing crop of chironomid larvae was noted for the sandy bottom types, whereas oligochaetes remained unchanged and Pisidium spp. decreased on sandy areas in

sector D (Table 3). The bottom fauna of the clay and mud showed very small changes between September and November.

Brundin (1949) in the summer of 1943 found about 1 600 chironomid larvae per m² in the deepest parts of the west lake and about 800 chironomid larvae per m² in a Ceratophyllum-meadow.

5. The diving duck populations of the lake

Lake Ringsjön is a resting area during spring and autumn and a moulting area in summer. Four species dominated markedly: Tufted Duck, Pochard, Goldeneye and Goosander. The Smew was a regular visitor in small numbers. Occasional observations have been made of the following species: Scaup, Long-tailed Duck, Eider, Somateria mollissima (L.) and Red-breasted Merganser, Mergus serrator L..

The Tufted Duck (Fig. 5) was noted in the area in large numbers during spring migration. Moreover, large numbers moulted in the lake and the highest counts were obtained during the first days of August. No counts were made in the summer of 1969 but in 1970 only a few specimens were seen in mid June whereas more than 1 000 were counted in mid July. The number of Tufted Ducks decreased during the autumn as the moulting birds, mainly males, departed for the coast, but a second peak was noted just before the lake was frozen.

The Pochard (Fig. 5) was sparse during spring migration but occurred in rather large numbers during autumn migration mainly in October. No moulting Pochards were seen in the lake.

The Goldeneye (Fig. 5) was noted in large numbers during spring migration in April and during autumn migration in late October and November. A moderate number of moulting Goldeneyes were found in early August. In 1970 only few Goldeneyes were seen in June, whereas the species was present in rather large numbers in mid July.

The Goosander (Fig. 5) was seen in large numbers during migration in April and November.

6. The local distribution of the diving ducks

The local distribution during autumn was studied in the three bottom-diving species, Tufted Duck, Pochard and Goldeneye. The fish-eating Goosander occurred all over the lake but approached the shore only for resting on the small island in the west lake.

The Tufted Duck was generally night-active in Lake Ringsjön as it was on the coasts of Scania but the proportion of day-active individuals was higher in the lake (Nilsson 1970). The main concentrations of the species in daytime were found along parts (sector A-C, mainly) of the shores in the west lake (Fig. 6). The resting flocks generally preferred the leeward side and the concentration areas were mostly situated outside the Phragmites-Scirpus belt with parts of the flocks lying just at the edge of the rushes. The flocks of Tufted Ducks in the west lake changed position during the season (Table 4) but showed no relation to the distribution of the bottom fauna (cf. Figs. 3 and 4). In sector N of the east lake most Tufted Ducks were counted on open water well off the shore but a large proportion of these birds were feeding in daytime. The largest flocks in August-September counted up to 500 birds. Outside the concentration areas only small groups were seen.

During daytime feeding Tufted Ducks were found only close to the shore and mainly in areas with sandy bottom. In the evening the resting flocks moved out to open water and dispersed over the lake. Tufted Ducks were obtained in nets from all over the west lake but mostly over the sandy bottom, especially in sector D. The whole west lake is well within the diving range of the species. In the east lake feeding Tufted Ducks were caught in nets at a depth of 9 m on muddy bottom.

In the Pochard three concentration areas were found in the west lake and two in the east lake (Fig. 6). During August and September, the majority of the few Pochards in the west lake were counted in sector F, where they stayed together with the more numerous Tufted Ducks and fed on shallow water with Chara-vegetation. The Pochards in sector C occurred mainly together with the Tufted Ducks, whereas only few Tufted Ducks were found in sector D, where the Pochards formed discrete flocks. The submerged vegetation besides Chara, mainly Potamogeton sp. in the west lake was virtually restricted to the western part where the majority of the Pochards were counted (Table 5).

The two concentrations in the east lake (sector G and K) were on shallow water with rather rich submerged vegetation.

The Goldeneye was a strictly day-active species so the feeding places could be established. In August-September only small numbers were found in the east lake scattered along the shores whereas in October-November somewhat more Goldeneyes were counted in this lake mainly on the shallow sandy areas in sector K or close to the shores in the other sectors. Many

were seen feeding just outside the Phragmites belt.

In the west lake the majority of the Goldeneyes were found in sector F (Table 6). This sector also showed the highest standing crops of the bottom fauna (Figs. 3 and 4, Tables 1 and 2). The other concentration areas were also found where the standing crop of the bottom fauna was higher than in the other areas. In sector A the Goldeneyes in August and September were almost all found in the richer eastern part with only occasional records in the other part of the sector. In sector D the Goldeneyes were feeding on the sandy bottom and not on the clay.

When comparing the distribution of the Goldeneyes in sector F in August-September and October-November a shift was found from feeding only rather close to the shore to feeding in deeper water (Fig. 6). In September the inner part of the sector had a higher standing crop than the outer sector but in October the situation was reversed (Table 2).

At night the Goldeneyes rested in flocks on open water some distance from the shore.

7. Food choice of the diving ducks

Two of the four Scaups obtained from the muddy bottom in the east lake in September had their stomachs filled with chironomid larvae. One stomach also contained 6 seeds of Scirpus lacustris and the other 10 seeds of Ceratophyllum demersum. According to Isakow in Dementiev & Gladkov (1952) insect larvae, molluscs and seeds have been found in stomachs of Scaups obtained from inland waters in the USSR (cf. also Cottam 1939).

Thirty Tufted Ducks from the west lake with food in their stomachs obtained in the autumns of 1968 and 1969 had a diet markedly dominated by bi-valves, mainly Pisidium spp. and Sphaerium corneum, and chironomid larvae (Fig. 7). Other food items found in any numbers included gastropods, i.e. Valvata cristata and Bithynia tentaculata, vegetable matter, seeds, insect remains and fishes. The seeds were mainly from Ceratophyllum demersum and Potamogeton spp. - found in single specimens in more than half of the stomachs - but seeds of Scirpus lacustris occurred in 4 stomachs and seeds of Carex spp. in one stomach, making up 3/5 of its content. The insect remains were mainly from Trichoptera or chironomid larvae, and 7 gizzards contained 1-5 larvae of Molanna (angustata) whereas a further 4 stomachs contained unidentified Trichoptera larvae. Fish remains (cypriid) were found to make up most of the content of one stomach. The one oesophagus had an unusually high number (185) of Sphaerium, a species scarce

in the bottom samples. Two specimens contained a few oligochaetes in the oesophagus whereas no oligochaetes were found in the gizzards.

Comparing the diet of the Tufted Ducks with the composition of the bottom fauna (Table 1) it is found that bivalves, mainly Pisidium spp. constituted a greater proportion of the diet in relation to the chironomid larvae than their relative abundance in the bottom fauna. Oligochaetes were rarely found in the stomachs although oligochaetes were an important item in the bottom fauna. They are however rapidly digested and will leave no resistant fragments and are therefore overlooked.

47 Tufted Ducks containing food were obtained from the east lake all being taken over muddy bottom in September-November. All had stomachs well filled with chironomid larvae but they only contained traces of other food items. Pisidium spp. were found in 6 stomachs. 1-8 seeds of Scirpus lacustris were found in 37 stomachs and Ceratophyllum demersum occurred in 2 stomachs.

A wide variety of food items have been reported for the Tufted Duck with animal food, mainly molluscs, dominating in most cases. For freshwater localities various insect larvae and seeds have also been reported as important items (Isakow in Dementiev & Gladkow 1952, Bauer & Blotzheim 1969, Madsen 1954, Olney 1963).

Only three Pochards containing food were obtained from the west lake. One had taken a few seeds of Ceratophyllum demersum, one had 68 seeds of Ceratophyllum demersum, 40 seeds of Potamogeton spp. and 8 seeds of Scirpus lacustris in the stomach and the third had exclusively fed on chironomid larvae as had one bird from the east lake.

The Pochard is reported to take more plant food than the Tufted Duck (Bauer & Blotzheim 1969, Isakow in Dementiev & Gladkow 1952, Madsen 1954, Olney 1968). Among the items reported as important may be mentioned various plants such as Chara spp. and Potamogeton spp., seeds of aquatic plants, and to a smaller extent animal food such as chironomid larvae, other insect larvae and molluscs. Willi (in Bauer & Blotzheim 1969) found chironomid larvae to be an important food item in a Swiss lake, tubificids also being an important food there.

Sixteen Goldeneyes from the west lake in September-November contained food (Fig. 8). The diet was markedly dominated by larvae of chironomids and Trichoptera, the unidentified insect remains probably mostly being larvae of Trichoptera. One stomach also contained some imagines of Trichoptera, probably taken from the water surface. Smaller amounts of mol-

luses, seeds and fish remains were also found. The molluscs identified included some Pisidium spp., 5 Bithynia tentaculata, and 4 Spiralina vortex. The dominating seed was Ceratophyllum demersum occurring in 11 stomachs and Scirpus lacustris occurring in 8 stomachs, but Carex sp. was also found. Other food items found included larvae of Sialis lutaria, larvae of Zygoptera, Hirudinea, Gammarus lacustris, Asellus aquaticus and one beetle (Coleoptera).

The large proportion of Trichoptera larvae in the diet was probably caused by the inclusion of a few Goldeneyes that had fed near the Phragmites-Scirpus areas, as Trichoptera larvae were not especially common on the main feeding grounds of the species (excl. Molanna). The Goldeneyes probably fed to a much larger extent on chironomid larvae than is showed in the diagram.

A wide variety of food items have been reported also for the Goldeneye. In freshwater localities the diet was usually dominated by larvae of various insects, e.g. Trichoptera, Plecoptera and Chironomidae. Other water insects, molluscs and fishes have also been reported (Cottam 1939, Bauer & Blotzheim 1969, Isakow in Dementiev & Gladkow 1952, Madsen 1954, Olney & Mills 1963).

One Long-tailed Duck from the west lake contained fish remains and one Smew from the same lake was full with remains of 36 Phryganea larvae (Trichoptera) plus single seeds of Potamogeton spp. and one Pisidium sp.

8. Exploitation of food resources

Stomach analysis give no idea of the amount of food taken by ducks, as it is not known how often the stomach is filled and how much has been digested since the bird started to feed. Longcore & Cornwell (1964) found the mean daily food-intake in autumn of captive Canvasbacks, Aythya valisneria Wilson, and Lesser Scaups, Aythya affinis Eyton, to be about 350 g and 200 g freshweight respectively when fed on a mixture of natural foods, mainly plants and molluscs. For the Eider, Gerasimova & Baranova (1960) estimated a daily food intake of 300 g of molluscs fresh weight. The amount of food taken will however vary with the kind of food taken and with the season.

The Tufted Duck and Goldeneye are between the Canvasback and Lesser Scaup in weight, so in a study of their exploitation of the food resources in a coastal area, where at least the Tufted Duck mainly feeds on molluscs, Nilsson (1969) put their daily food consumption to 200 g fresh weight in the calculations. This value will also be used here but it must be

remembered that it is only a rough estimate that will give the order of size.

Between the start of the observations in early August and late November 1969, when the lake was ice-covered, the west lake was exploited by 125,800 bird-day units. With a consumption of about 200 g per day the total consumption of the diving ducks in the lake was ca 26 metric tons compared to a total standing crop of suitable food species in September of about 82 tons (Table 1). In the most extensively used sector of the lake, F, the total consumption was 7 tons compared to a standing crop of ca 30 tons in September.

The production of food was good during the autumn and there was an increase in the standing crop of chironomid larvae, the most important food item, in spite of the predation by ducks and other animals, e.g. fish (Tables 2 and 3).

One important food item, Pisidium spp., taken in quantities by the Tufted Ducks, showed a decrease during the autumn (Tables 2 and 3). In sector F it decreased from 6.0 to 2.8 g/m² on the inner parts between 9 September and 22 October, equalling 8,700 bird-day units taking 200 g per day. From 22 October to 25 November only a slight change occurred, but the area was not used by any numbers of Tufted Ducks during that period. Similarly in sector D the standing crop of Pisidium spp. decreased from 1.7 g to 0.1 g per m² between the beginning of September and 22 November. This equals a consumption of 200 g per day by 5,700 bird-day units. Since sector D was much used by the Tufted Ducks for feeding and as Pisidium spp. seemed to be their preferred food, the decrease in standing crop was probably due to the activity of the ducks.

9. Discussion

The factors that influence the habitat selection of diving ducks in coastal areas of south Sweden are discussed elsewhere (Nilsson in prep.). Szijj (1965) treated the factors influencing the choice of places for various activities in anatids (cf. also Hildén 1965 for a general discussion of habitat selection in birds).

Lake Ringsjön serves mainly two functions for diving ducks. It was a moulting area for Tufted Ducks and to a lesser degree for Goldeneyes and it was a resting area during migration for these species, Pochard and Goosander.

A moulting area for ducks must offer protection for the ducks during the flightless period and a sufficient quantity of available food (cf. Bozzel

1964, Szijj 1965). According to Bezzel (l.c.) the diving ducks prefer to stay on open water with a depth of more than 1 m during the moult, whereas the Anas species moult in cover.

A resting area for diving ducks must also offer sufficient quantities of food plus suitable resting places for the inactive periods.

Lake Ringsjön fulfils all these requirements. As found above the available food quantities in the west lake were sufficient for a considerably larger population. In fact the ducks had no noticeable effect on the bottom fauna apart from the probable influence of the Tufted Ducks' predation on Pisidium spp.. This certainly applies also to the east lake which was used by fewer ducks than the west lake (Fig. 5) despite its being the larger of the two. No single food item will be limiting for the diving ducks as they will easily turn to another food item when their preferred food becomes scarce.

The moulting ducks also find large open areas of water of suitable depth, where they can easily detect any intrusion in good time and escape by diving. Moreover quiet resting places are available in daytime for the night-active species along the shores.

Proximate factors governing the choice of feeding places of the diving ducks include: rich food supply, the depth of the water, lack of disturbance on the feeding places and social factors (cf. Szijj 1965). In Lake Ringsjön areas with rich food supply coincided with shallow water where the food is easily reached. In sector F lack of disturbance was added to rich food supply and shallow water and the sector was accordingly used by most Goldeneyes in the west lake. Social factors were also important and most feeding ducks were seen in groups and often the ducks were concentrated to parts of a rich area where their exact localization shifted between different days.

Proximate factors for the selection of resting places will probably include the distance from the shore. Goldeneyes were always found resting some hundred metres off the shore, whereas Tufted Ducks and Pochards often stayed closer to the shore, where the water was calmer. Social factors were also important as the ducks gathered in flocks for resting. Moreover the few Pochards in early autumn were mainly associated with the more numerous Tufted Ducks.

10. Acknowledgements

The work was carried out at the Department of Animal Ecology of the University of Lund and I wish to express my sincere gratitude to Professor P. Brinck, Head of the Department, for working facilities and valuable advice. Thanks are also due to Messrs. S. Bergström and B. Ohlsson for putting ducks at my disposal for stomach analysis and to Mr. E. Bengtsson of the Hälsingborg Stads Vattenverk for giving me access to maps of the bottom types of Lake Ringsjön.

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Table 1. Standing crop (g/m^2 wet-weight in 80 % alcohol) of the macrofauna of different bottom types in the sectors of the west Ringsjö lake on September 4-9, 1969. Mean values $\pm$ standard error for all samples in each division.

Sector	Bottom-type	Area (ha)	No of sampl.	Standing crop (g/m^2)			Total	Total estimated standing crop of sector (tons)
				Chirono- mid larvae	Oligo- chaetes	Pisidium spp.		
A: east	Sand+stones	30	20	8.0 ± 2.7	1.8 ± 0.3	2.5 ± 0.6	15.2 ± 3.2	4.5
west	Sand+mud+ stones	24	12	0.4 ± 0.1	+	+	0.9 ± 0.2	0.2
	---	30	15	0.8 ± 0.3	0.3 ± 0.1	1.2 ± 0.5	3.3 ± 0.9	0.9
	sand+mud	53	30	3.1 ± 0.5	4.1 ± 0.8	1.7 ± 0.3	12.3 ± 1.6	6.5
D	clay	7	9	1.0 ± 0.4	1.1 ± 0.4	0.5 ± 0.3	5.4 ± 1.5	0.4
	sand	71	29	4.3 ± 0.9	3.0 ± 0.5	1.4 ± 0.4	9.6 ± 1.4	6.8
	clay	47	6	0.3 ± 0.1	1.6 ± 0.6	0.2 ± 0.1	3.3 ± 1.1	1.6
E	sand	97	39	3.9 ± 0.4	2.0 ± 0.3	1.3 ± 0.3	7.8 ± 1.7	7.5
F	inner fine sand	58	49	5.3 ± 0.9	9.9 ± 0.8	6.0 ± 0.7	22.7 ± 1.8	13.1
	outer sand	107	54	9.6 ± 1.3	3.3 ± 0.3	2.0 ± 0.3	15.8 ± 1.6	16.8
Mid-lake	mud	835	50	2.4 ± 1.3	+	+	2.8 ± 1.6	23.6
Total		1359	313					81.9

Table 2. Standing crop (g/m^2 wet-weight in 80 % alcohol) of the macrofauna of the inner and outer part of sector F on three occasions in the autumn of 1969. Number of samples in brackets. Means $\pm$ standard error for all samples.

Item	September 9	October 22	November 25
Inner sector	(49)	(50)	(50)
Chironomidae	5.3 ± 0.9	7.8 ± 0.9	8.7 ± 1.0
Oligochaeta	9.9 ± 0.8	8.1 ± 0.7	6.7 ± 0.7
Pisidium spp.	6.0 ± 0.7	2.8 ± 0.3	2.2 ± 0.3
All items	22.6 ± 1.8	19.5 ± 1.4	18.1 ± 1.1
Outer sector	(54)	(50)	(30)
Chironomidae	9.6 ± 1.3	16.3 ± 1.4	14.3 ± 1.7
Oligochaeta	3.3 ± 0.3	5.3 ± 0.5	5.3 ± 0.7
Pisidium spp.	2.0 ± 0.3	2.4 ± 0.3	1.7 ± 0.3
All items	15.8 ± 1.6	24.2 ± 1.4	21.7 ± 2.1

Table 3. Standing crop (g/m^2 wet-weight in 80 % alcohol) of the macrofauna in sectors C and D of the west lake on two occasions in the autumn of 1969. Number of samples in brackets. Means $\pm$ standard error of all samples in each bottom type and division.

Sector and bottom type		Item	September 4-9	November 22
C	Sand+mud		(21)	(20)
		Chironomidae	2.6 ± 0.5	9.9 ± 1.6
		Oligochaeta	5.3 ± 1.0	4.8 ± 0.7
		Pisidium spp.	2.4 ± 0.4	3.0 ± 0.5
		All items	14.3 ± 2.1	20.2 ± 2.1
C-D	Mud		(23)	(15)
		Chironomidae	0.8 ± 0.2	0.7 ± 0.1
		All items	1.0 ± 0.2	1.1 ± 0.1
D	Sand		(20)	(20)
		Chironomidae	4.7 ± 1.3	20.0 ± 1.6
		Oligochaeta	2.9 ± 0.4	3.5 ± 0.6
		Pisidium spp.	1.7 ± 0.5	0.1 ± 0.02
		All items	9.9 ± 1.7	26.0 ± 1.7
D	Clay		(9)	(20)
		Chironomidae	1.0 ± 0.4	1.3 ± 0.3
		Oligochaeta	1.1 ± 0.4	0.8 ± 0.2
		Pisidium spp.	0.5 ± 0.3	+
		All items	5.4 ± 1.5	2.9 ± 0.7

Table 4. Percentage distribution of Tufted Ducks, Aythya fuligula, in sectors of the west lake in different months in 1969. Number of counts in brackets.

Sector	April (5)	August (2)	September (4)	October (4)	November (4)
A	22	26	26	8	22
B	24	44	8	8	14
C	25	7	25	56	56
D	13	+	2	7	4
E	8	+	6	9	4
F	8	23	33	12	+
Total numbers counted	1523	2192	1322	2011	1897

Table 5. Percentage distribution of Pochards, Aythya ferina, in sectors of the west lake in different months in 1969. Number of counts in brackets.

Sector	April (5)	August (2)	September (4)	October (4)	November (4)
A	20	12	9	1	-
B	20	16	9	+	-
C	-	8	17	40	66
D	25	-	1	24	34
E	15	-	-	18	-
F	20	64	64	17	-
Total numbers counted	41	25	233	881	350

Table 6. Percentage distribution of Goldeneyes, Bucephala clangula, in sectors of the west lake in different months in 1969. Number of counts in brackets.

Sector	April (5)	August (2)	September (4)	October (4)	November (4)
A	14	18	8	3	7
B	26	19	16	6	7
C	14	4	8	20	6
D	11	-	3	12	22
E	2	+	4	9	7
F	33	59	61	50	51
Total numbers counted	1778	407	522	1731	2161

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Table 7. Estimated exploitation of the bottom fauna of the west Ringsjö lake in 1969 by the diving ducks.

Area and period	Number of bird-day units				Bird-days per m ²	Mean consumption g/m ² with a con- sumption of 200 g/bird/day
	Aythya fuligula	Aythya ferina	Bucephala clangula	Total		
<u>Whole lake (1359 ha)</u>						
Spring	16,600	400	18,400	34,800	0.0025	0.5
Autumn (Aug.-Nov.)	71,900	14,300	39,600	125,800	0.0093	1.9
Sept.-Nov.	39,100	12,000	32,900	84,000	0.0061	1.2
<u>Sector F (165 ha)</u>						
Spring	1,350	—	6,850	8,200	0.0049	1.0
Autumn (Aug.-Nov.)	11,530	2,710	21,080	35,320	0.021	4.2
Aug.-Sept.9	7,240	600	3,940	11,780	0.0072	1.4
Sept.9-Oct.22	3,450	1,540	4,840	9,830	0.0060	1.2
Oct.22-Nov.25	840	570	12,300	13,710	0.0083	1.6

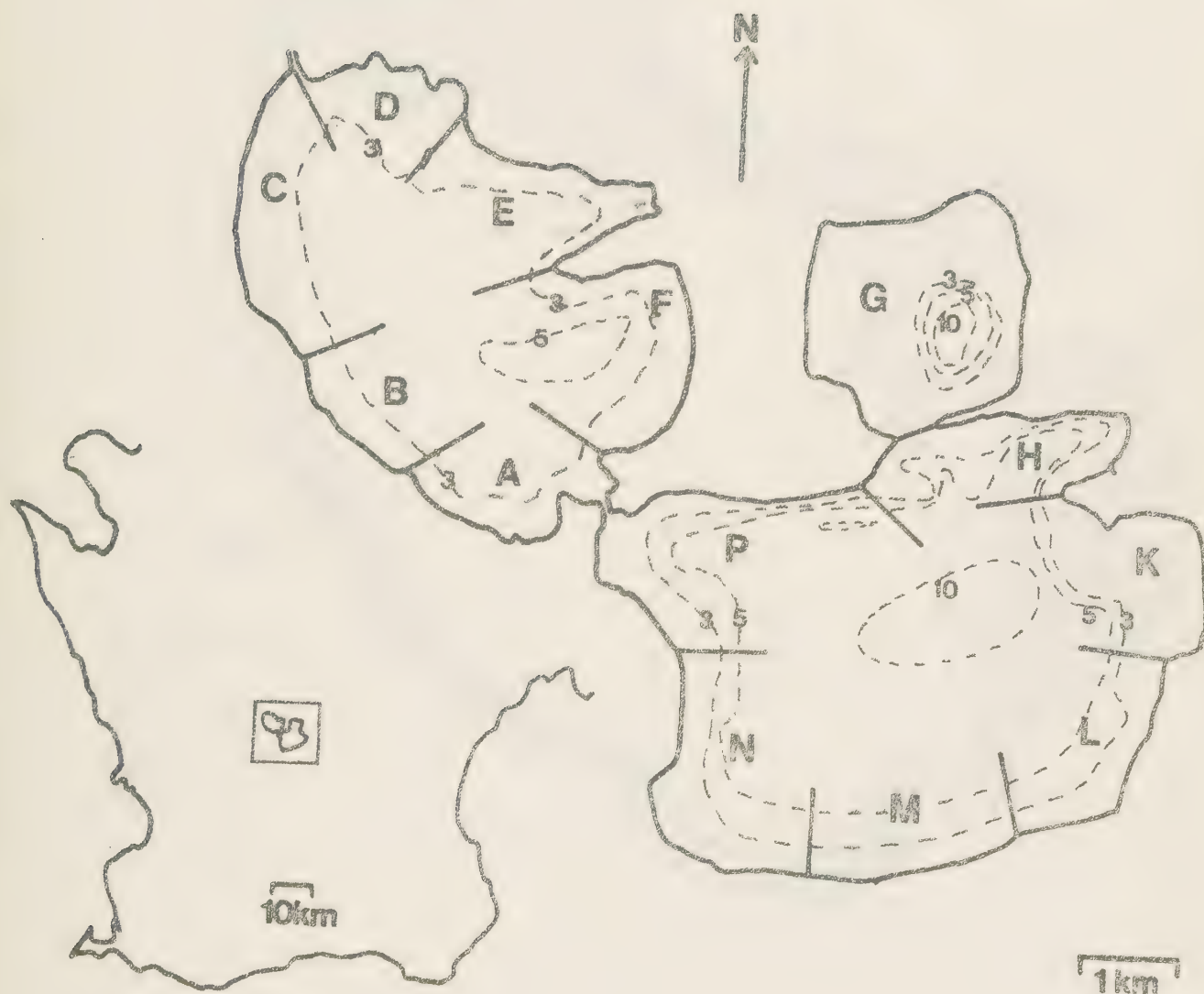


Fig.1. The study area in southernmost Sweden (lower) and the general outline and the division into sectors of the lakes (upper). Broken lines show depths of 3, 5 and 10 m.

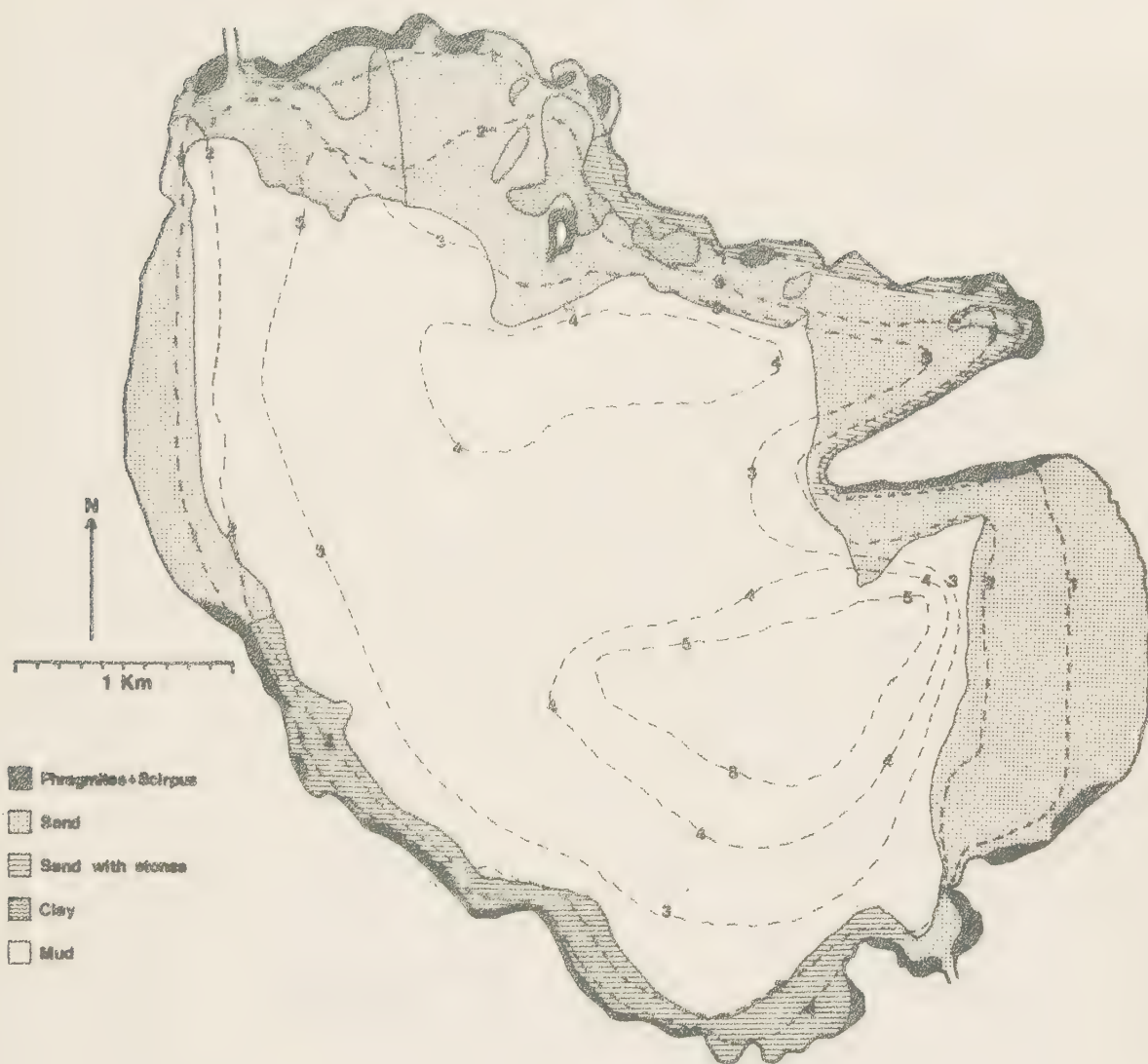


Fig.2. The different bottom types and emergent vegetation of the west lake.
Broken lines are depth curves.



Fig.3. Standing crop (g/m² wet-weight in 80 % alcohol) of chironomid larvae on different stations in the west lake, September 4-9 1969.



Fig.4. Standing crop (g/m^2 wet-weight in 80 % alcohol) of the macro-fauna on different stations in the west lake ,September 4-9 1969.

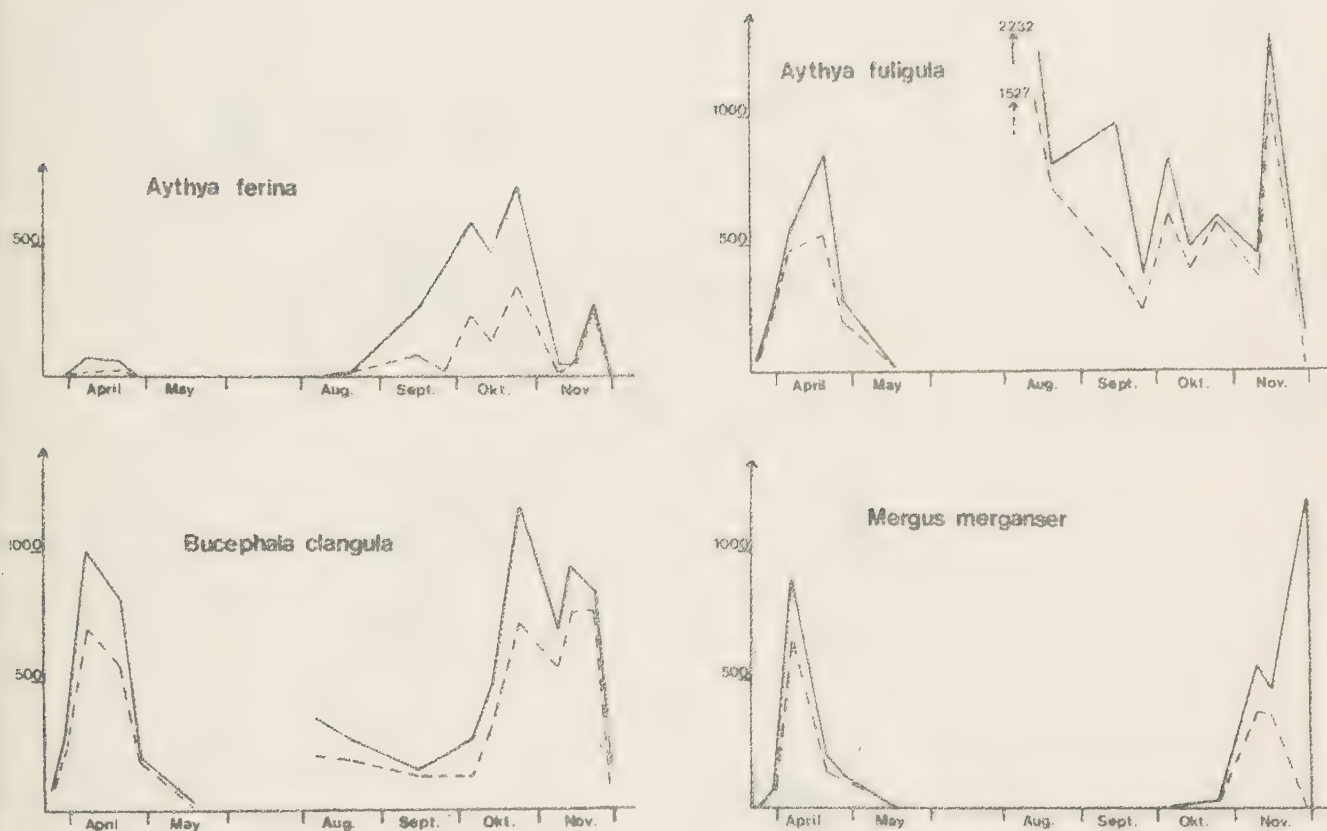


Fig.5. Number of resting diving ducks on Lake Ringsjön in 1969. The broken curve show numbers counted on the west lake alone.

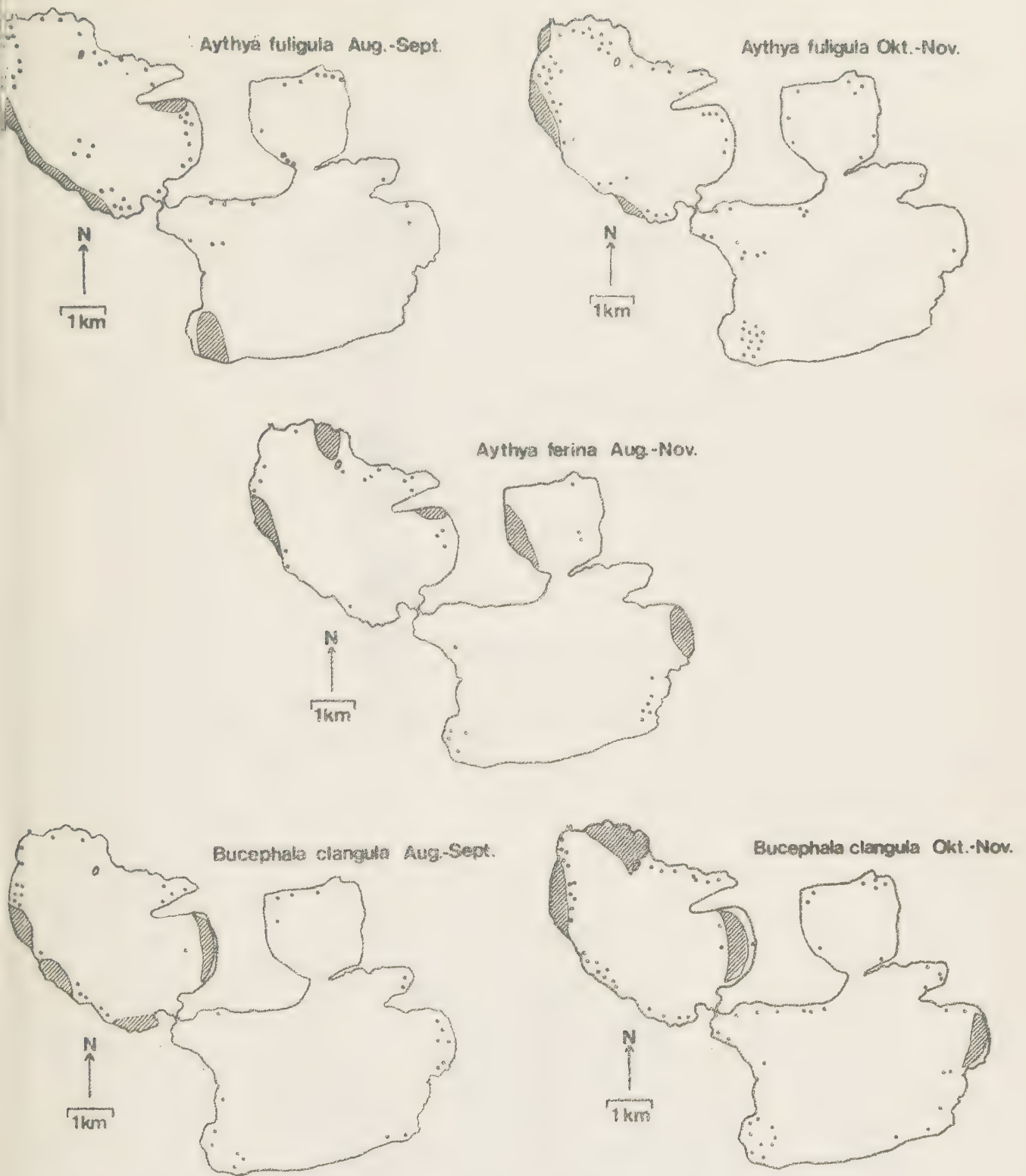


Fig.6. The daytime distribution of Tufted Duck, *Aythya fuligula*, Pochard, *Aythya ferina*, and Goldeneye, *Bucephala clangula*, on Lake Ringsjön, August-November 1969. Areas used by larger numbers of ducks hatched, dots = single occurrences.

	Chironomidae larvae
	Trichoptera larvae
	Insect fragments
	Bivalvia spp.
	Gastropoda spp.
	Pisces spp.
	Seed
	Vegetative remains
	Rare food items

Key to Figs. 7 and 8.

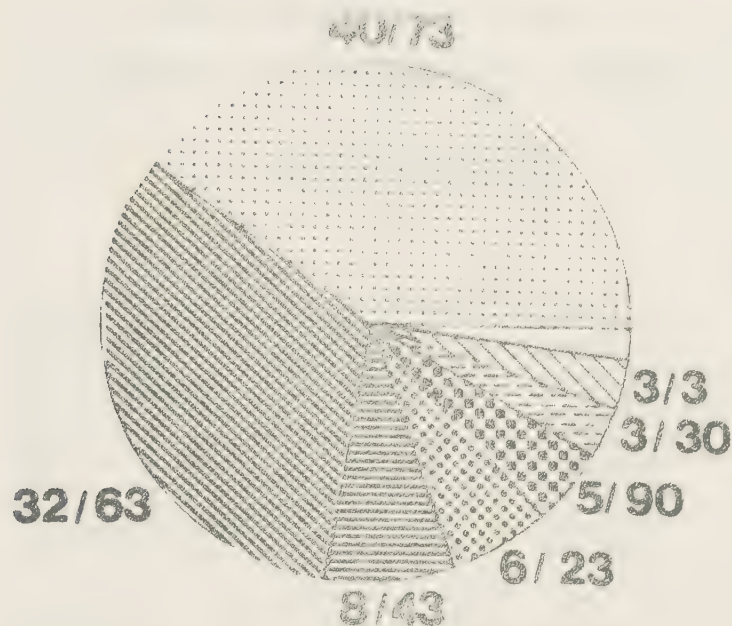


Fig.7. The diet of 30 Tufted Ducks, *Arthya fuligula*, from the west lake in autumn 1968 and 1969. The width of the sectors denote the percentage of the various food items according to the estimation method (first figure) and the second figure the frequency of occurrence of the item.

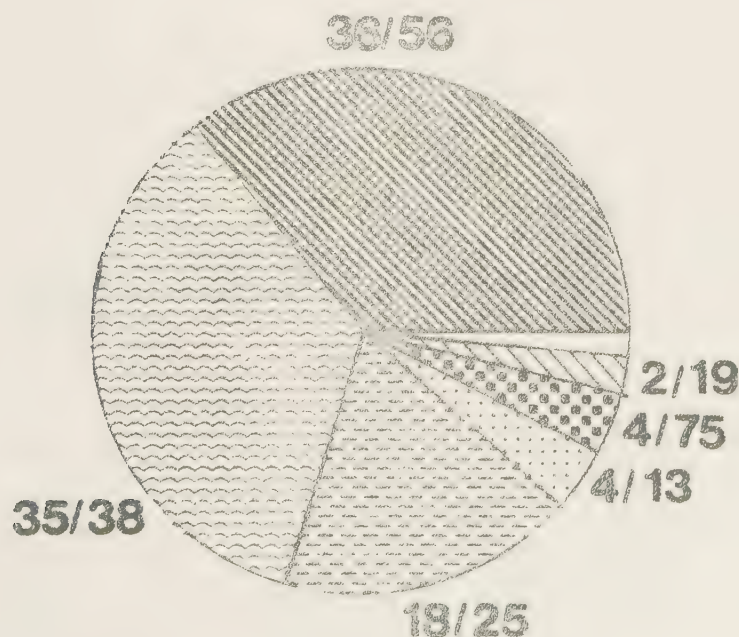


Fig.8. The diet of 16 Goldeneyes, *Bucephala clangula*, from the west lake in autumn 1968 and 1969. For further explanation see Fig.7!

Food consumption of diving ducks wintering at the coast of South Sweden in relation to food resources

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Abstract

The food choice of diving ducks in the non-breeding season and their exploitation of the potential food resources were investigated in an area on the Scania coast of the Sound (Öresund) in 1965/66 and 1966/67. *Aythya marila*, *A. fuligula* and *Bucephala clangula* occurred commonly in the area together with a few *Somateria mollissima*, all feeding in shallow water (below 3 m) with *Zostera* meadows and muddy bottom. 24 *A. marila* from March and April showed a marked preference for *Mytilus edulis* in the food. 63 *A. fuligula* from September–March showed a seasonal variation in the composition of the food related to partly different feeding places in the different months. In autumn and spring *Cardium lamarckii* and Hydrobiidae spp. dominated the food, whereas *Mytilus edulis* was more common in December.

The exploitation of the food resources of the 410 ha large area was calculated from regular censuses. 172,000–213,000 bird-day units were recorded which, with an estimated consumption of 200 g food/bird/day, equals a consumption of 8–10 g/m² fresh weight. The consumption by the diving ducks from November to April 1966/67 was about 5 ± 2% of the total decrease in standing crop of potential food species calculated from quantitative bottom samples compared with a total decrease in standing crop of about 70%.

Резюме

Питание зимующих уток и их использование потенциальных кормовых ресурсов исследовались в районе шведского берега пролива Эресуна в 1965–66 и 1966–67 гг. В этом районе встречаются *Aythya marila*, *Aythya fuligula*, *Bucephala clangula* и единичные *Somateria mollissima* которые ищут корм на небольшой глубине (до 3 метров) с *Zostera* или глинистым дном. В пище 24 пойманных в марте–апреле *Aythya marila* в большом количестве был обнаружен *Mytilus edulis*. В пище 63 *Aythya fuligula* пойманных от сентября до марта замечалась сезонная перемена в связи с разными местами кормления. Осенью и весной преобладали *Cardium lamarckii* и Hydrobiidae spp., а *Mytilus edulis* встречался чаще в декабре.

Использование площади для поисков корма в 410 га высчитывалось благодаря регулярной инвентаризации. Было насчитано 172,000–213,000 птица/дней. В результате это дает приблизительно 200 г корма в один день на одну птицу и отвечает 8–10 г/м² свежей массы. Потребление корма зимующими утками составляет осенью около 5 процентов общего уменьшения кормовых организмов, зимой 1966/67 общее уменьшение на 70 процентов.

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OIKOS 20, 1 (1969)

1. Introduction

Numerical fluctuations of wintering diving ducks have been intensively studied in recent years, but little work has been done on their habitat selection and food habits (cf. e.g. Madsen 1954, Szijj 1965). The food choice in relation to the available food resources has not been studied, but this aspect was treated by Geramisova and Baranova (1960) in a study of breeding Eiders (*Somateria mollissima* L.).

The purpose of the present investigation was to compare the food choice and food consumption of the diving ducks with the food resources available. The field work of the study was performed mainly during September–April in 1965/66 and 1966/67.

2. Study area

The investigations were carried out in the Bjärred area at the South Swedish coast of the Sound 10–15 km N of Malmö. The area is characterized by extensive areas of shallow water showing a zonation of three main bottom types (Fig. 1): 1) Muddy bottom with low vegetation of *Zostera marina* L., *Ruppia* sp. and *Zannichellia* sp. and a maximum depth of 0.5–1 m. 2) A belt of vegetation-free sand at a depth of about 0.5–1 m. 3) Meadows of *Z. marina* with an innermost limit at a depth of 1 m. In the northern parts of the area the bottom consists of silt deposited by the River Kävlingeån and is without vegetation.

3. Methods

Quantitative samples of the bottom fauna were taken at several stations. The bottom fauna of the muddy bottom and in the *Zostera* zone was sampled in autumn and spring (the vegetation-free sand had no fauna of importance for the diving ducks) on fixed stations well dispersed over the area. Four samples were taken at each station and occasion, using a mud-sampler taking 0.03 m². A sieve with

OIKOS 20, 1 (1969)

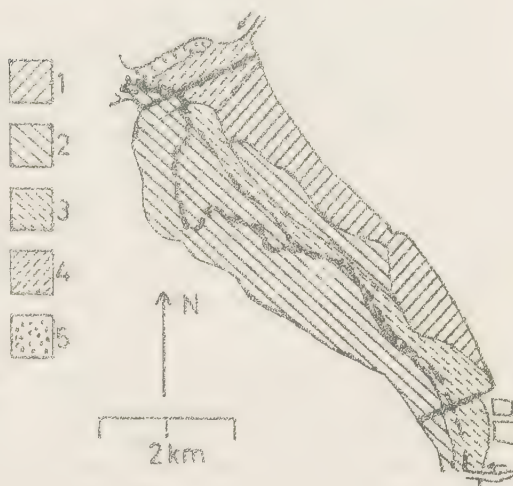


Fig. 1. Bottom types of the study area (bordered by thick lines), Bjärred at the coast of western Scania, out to a depth of 6 m. 1 = muddy bottom, 2 = *Zostera* zone, 3 = vegetation free sand, 4 = vegetation free silt, 5 = stony bottom. The 3 m depth contour is shown by a thick broken line.

1 mm meshes was used. The samples were brought alive into the laboratory for sorting and were preserved in 80% alcohol. Before weighing they were dried between filter papers.

24 Scaups (*Aythya marila* L.), 63 Tufted Ducks (*Aythya fuligula* L.) and 1 Goldeneye (*Bucephala clangula* L.) were collected by shooting in the morning flights from the feeding grounds to the resting place and from fishermen who caught ducks in their nets. The gizzard and the oesophagus of the collected birds were removed and preserved in 80% alcohol and their contents analysed separately. The oesophagus contents were sorted and identified to species and weighed after drying between filter papers. The gizzard contents were identified to species as far as possible and the proportions of the various food items were estimated in tenths of the total gizzard content. From these estimates the percentage

Tab. 1. Standing crop of the macro-fauna in the Bjärred area, the Sound, in 1966/67 (g/m² wet-weight in 80 % alcohol). Only the important food species are shown separately. The values are given with standard error.

	Mud (20 samples)			Zostera (16 samples)		
	22.9	17.11	4.4	22.9	17.11	4.4
Crustacea total . .	10.8 ± 1.4	10.8 ± 1.5	4.6 ± 0.7	19.2 ± 3.5	13.5 ± 1.7	8.5 ± 1.1
<i>Nereis diversicolor</i>	44.3 ± 8.5	21.1 ± 5.9	25.4 ± 4.0	29.6 ± 4.9	17.2 ± 4.4	19.5 ± 1.7
Mollusca total . .	38.0 ± 7.7	29.5 ± 7.2	6.4 ± 2.0	95.5 ± 27.8	298 ± 36	80.4 ± 15.5
<i>Mytilus edulis</i> .	Patchy distribution on the mud			45.8 ± 21.1	238 ± 72	65.9 ± 15.0
<i>Cardium</i>						
<i>lamarckii</i>	13.0 ± 5.1	13.0 ± 4.9	3.5 ± 1.9	37.6 ± 10.4	32.4 ± 8.5	9.9 ± 2.0
Hydrobiidae						
spp.	17.1 ± 4.5	8.9 ± 1.2	2.2 ± 0.7	8.1 ± 1.9	10.3 ± 3.2	1.1 ± 0.2
Crustacea +						
Mollusca	48.8 ± 8.2	40.3 ± 8.0	11.0 ± 2.5	115 ± 29	311 ± 37	88.9 ± 16.0

composition of the food was calculated. No significant differences between the composition of oesophagus contents by weight % and between the composition of the gizzard contents according to the method described above were found. The reliability of the two methods will be discussed elsewhere (Nilsson in).

The feeding areas of the day-active ducks were established from field observations of the feeding flocks partly using observations from two points to obtain the position of the flock. In the night-active species the evening flights to the feeding grounds were followed, moreover data were obtained from fishermen catching diving ducks in their nets.

Almost weekly counts were made of the diving ducks in the area to establish the size of the populations in different parts of the season and the use made of the area by the feeding ducks in terms of bird-day units (number of birds × number of days) was estimated from graphs of the seasonal variation in numbers of the commonest species.

4. The bottom fauna of the study area

At the quantitative sampling in 1966/67 (Tab. 1) only more abundant species of the macro-fauna were considered. Marked differences occurred between the two bottom types. The fauna of the *Zostera* zone was dominated by *Mytilus edulis* L., whereas the fauna of the muddy bottom was dominated by *Cardium*

lamarckii Reeve, Hydrobiidae spp. and *Nereis diversicolor* O. F. Müller. Among species not shown separately in the table (= not important as food species for the ducks) *Gammarus*, *Idothea* and *Cyathura carinata* (Kröyer) dominated among the crustaceans. Moreover the *Littorina* sp. that was taken as food by the ducks occurred only locally. Comparing the samples taken in autumn and spring a marked decrease in the total standing crop and in the standing crop of most species was found. For hydrobiids and *C. lamarckii* it decreased to about 10 and 20 %, respectively, of the autumn values. The overall decrease from September/November to April for all species considered was about 70 % for both bottom types. In hydrobiids a marked decrease in the standing crop was found between September and November.

The samples taken in 1965/66 (on different positions at the different occasions) showed a similar composition of the bottom fauna as the samples in 1966/67 but the standing crop was somewhat higher in the samples from both bottom types. Moreover, the decrease between autumn (October) and spring (April) was markedly lower than in 1966/67 amounting to about 40 % for the *Zostera* zone and even lower for the muddy bottom. The protection from ice in 1965/66 that covered most parts of the shallow areas from January to mid-March was probably of importance in this respect.

Food consumption of diving ducks

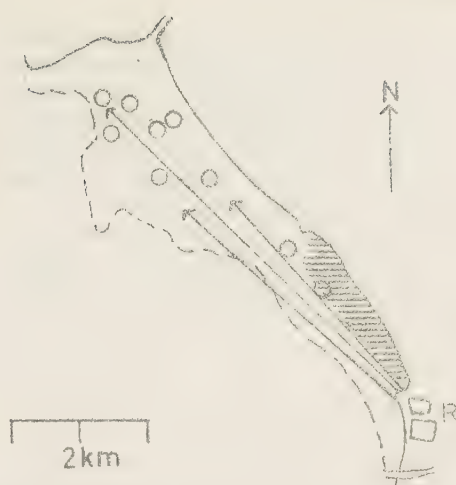


Fig. 2. Feeding area of the Tufted Duck (*Aythya fuligula*). Arrows show the directions of feeding flights from the resting place (ponds at R), circles show places where flocks were seen to settle on the water for feeding or where Tufted Ducks were obtained in nets. The hatched area was used for resting and feeding in spring when the ponds were frozen.

5. Feeding areas of the diving ducks

The Bjärred area is exploited for feeding by numerous Tufted Ducks and Goldeneyes all through the winter season, normal maximum numbers being 1,500 and 600 respectively, and by a flock of 200-400 Scaups mainly in late winter and spring. The area is also used by small numbers of feeding Eiders.

The Tufted Duck and the Scaup are night-active, resting on two ponds near the area in daytime and making regular flights to the feeding grounds after sunset (Fig. 2). Feeding Tufted Ducks were frequently caught in nets, often in considerable numbers, both over the muddy bottom and the *Zostera* zone (over the latter mainly in winter). These records and positions of flocks alighting on the water were all from the area inside the 3 m depth contour (Fig. 2). The Scaups occurred mainly together with the Tufted Ducks resting in mixed flocks. When the ponds were frozen the Tufted Ducks and the Scaups left the area, but they returned in spring before the ponds were free of ice and rested then in a restricted part of the sea

OIKOS 20, 1 (1969)

near the shore where they were also seen feeding in daytime. Some differences in feeding areas occur between the Scaups and the Tufted Ducks as is evident from the discussion of their food choice; the Scaups apparently feed mainly over the *Zostera* bottom.

The Goldeneye is a diurnal feeder that occurred well dispersed over the muddy bottom and the inner *Zostera* zone (Fig. 3) but only in small numbers over the outer *Zostera* zone, mainly when the innermost areas were frozen. The Goldeneyes stayed in the area except when it was completely ice-covered.

The Eiders were almost always seen feeding over the *Zostera* bottom.

Thus the diving ducks used the same general feeding area mainly on the shallow water within the 3 m depth contour, but with some differences as stated above, the main one being between the night-active and day-active species.

6. Food choice of the diving ducks

The Scaups were all shot on the morning flights in March and April with their stomachs

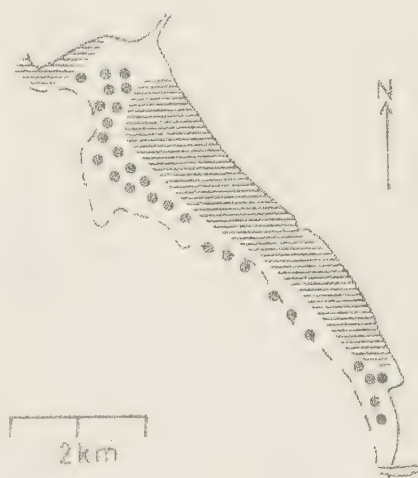


Fig. 3. Feeding area of the Goldeneye (*Bucephala clangula*). The hatched area is the main feeding area and dots mark areas less frequently used, i.e. mostly when the innermost areas are frozen.

well filled by food, and showed a marked dominance for *Mytilus edulis* and *Macoma baltica* L. in their diet (Fig. 4). One bird contained *Cardium lamareckii* in large numbers. Besides the dominant food items a few specimens of *Mya arenaria* L., Hydrobiidae spp., *Gammarus* sp., *Idothea viridis* Slabber and *Crangon crangon* L. were found. A similar composition of the diet was found by Madsen (1954) for Scaups from the Danish side of the Sound. It is clear that the Scaups from the Bjärred area obtained most of their food from the *Zostera* zone.

In the Tufted Duck four items made up almost the total food in the Bjärred area: *Mytilus edulis*, *Cardium lamareckii*, Hydrobiidae spp. and *Litorina litorea* L. In general one or two components dominated the entire meal with the other species being more occasionally taken. Smaller amounts of *Mya arenaria*, *Gammarus* sp., *Idothea viridis*, *Corophium* sp., and *Sphaeroma* sp. were also found in the stomachs. A marked seasonal variation in the food was found (Fig. 5). In September, hydrobiids and *C. lamareckii* dominated. Later in the season *M. edulis* was more common and dominated in December, whereas hydrobiids again dominated in March. *C. lamareckii* occurred to a much smaller extent in the food in March than in the other months, but it was commoner than the hydrobiids on the feeding grounds in April.

The food choice in autumn and spring corresponds to the general composition of the mollusc fauna of the muddy parts of the area whereas the composition of the diet in December corresponds to the fauna of the *Zostera* zone. Thus the change is probably related to a shift in the feeding sites. This is supported by the fact that Tufted Ducks were only caught in nets in the *Zostera* zone during the winter whereas they were frequently caught over the mud in autumn and spring.

As shown above, marked differences occurred in the food choice between the Scaup and Tufted Duck for March–April, the only months in which Scaups were available for analysis. *M. edulis* dominated the food of the Scaup to an extent of about 70% whereas the Tufted Duck had only 25% *M. edulis* in its

food relying mainly on hydrobiids. In other areas of the Öresund and the Baltic lacking the shallow muddy areas of the Bjärred area the Tufted Ducks had a much higher proportion of *M. edulis* in their diet, which was then similar to that of the Scaup (cf. Madsen 1954, Nilsson in prep.).

Only one Goldeneye was obtained for analysis owing to the shyness of the species. The specimen obtained (drowned in a net) was well filled with *Gammarus* sp., *Idothea viridis* and hydrobiids. Goldeneyes obtained from the Baltic coast of Scania had a diet markedly dominated by *M. edulis* with smaller amounts of *Litorina* sp., *Gammarus* spp., *Idothea baltica* and some fishes. A similar diet was found in the Danish localities of the Sound and the Baltic whereas Goldeneyes in the Danish fjords also consumed considerable numbers of seeds of various kinds (Madsen 1954).

The Eiders in the Sound and the Baltic feed mainly on *M. edulis* (Madsen op. cit.).

7. Exploitation of food resources

The food consumption of the ducks cannot be ascertained from the stomach analysis as it is not known when the food was consumed and how much was already digested when the birds were shot. Moreover, it is not known how often the birds fill their stomachs.

The largest food content in an oesophagus of a Tufted Duck was 44 g plus some food in the gizzard, i.e., about 50 g of molluscs (fresh weight). Belopolski (1957) and Pertsov (1951), vide Gerasimova and Baranova (1960), considered a single intake of the Eider to be 70–80 g of molluscs and multiplying with the number of intakes per day arrived at a daily consumption of 300 g of molluscs fresh weight (i.e., about 15–20% of the body weight). Longcore and Cornwell (1964) found the mean consumption of captive Canvasbacks (*Aythya valisneria* Wilson) and Lesser Scaups (*Aythya affinis* Eyton) fed on a mixture of natural food, mainly plants, to be 350 g and 200 g, respectively, equivalent to 30–40% of their body weights. The Scaup, Tufted Duck and the Goldeneye are between the Canvasback

Food consumption of diving ducks

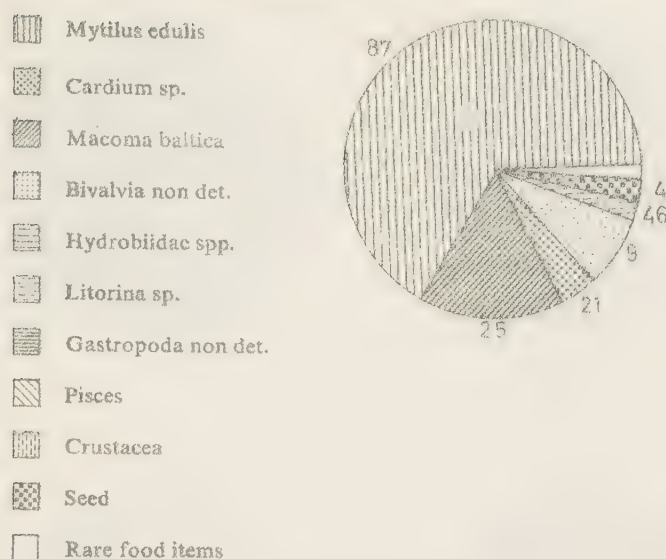


Fig. 4. Composition of the diet of 23 Scaups (*Aythya marila*) collected during the morning flights in March–April 1967 and 1968. The width of the sectors show the percentage of each major food item and the figures indicate their frequency of occurrence.

and Lesser Scaup in weight but they take mainly mollusc food and are thus more comparable to the Eider. Consequently the food consumption used in the calculations here was set to 200 g (20–35 % of the body weight). As stated above the Eider takes more, but it is of little importance compared with the other three more numerous species.

By using this value and the bird-day units calculated from the counts of the ducks, the general food consumption per m² was calculated considering the total area of muddy bottom and *Zostera* within the 3 m depth contour as the feeding area, i.e. 410 ha (Tab. 2). As stated above almost all feeding was confined to this area, but as the Scaups and Tufted Ducks feed at night it was not possible to get an exact delimitation of their feeding areas. In the Goldeneye, however, most feeding occurred in the area inside the sandbanks, total area 310 ha. The actual exploitation is thus heavier than stated in the table for the most frequented areas. Similar values were calculated for other areas in the Sound and on the Baltic coast of Scania, whereas a con-

sumption of 36 g/m² was found for an area outside Malmö that had a rich fauna near a sewage outlet.

The quantitative samples of the bottom fauna (Tab. 1) can be used to make a rough estimate of the exploitation of the food-resources by the diving ducks. Using the values for the standing crop (g/m²) and multiplying by the area of the bottom types (230 ha for the mud, 80 ha for the *Zostera* inside the sandbanks and 100 ha for the *Zostera* outside the sandbanks out to a depth of 3 m) the total potential food resources at November 17. were estimated to be 340 ± 60 metric tons for the area inside the sandbanks and 650 ± 85 tons for the total area inside the 3 m depth contour. The respective values for April 4. were 96 ± 18 tons and 185 ± 35 tons. The errors given in these estimates are the added standard errors of the estimates for the respective bottom types. Between the two sampling occasions the total food resources decreased with 244 ± 78 tons and 465 ± 120 tons respectively or about 70 %. The estimated total food consumption by the diving ducks

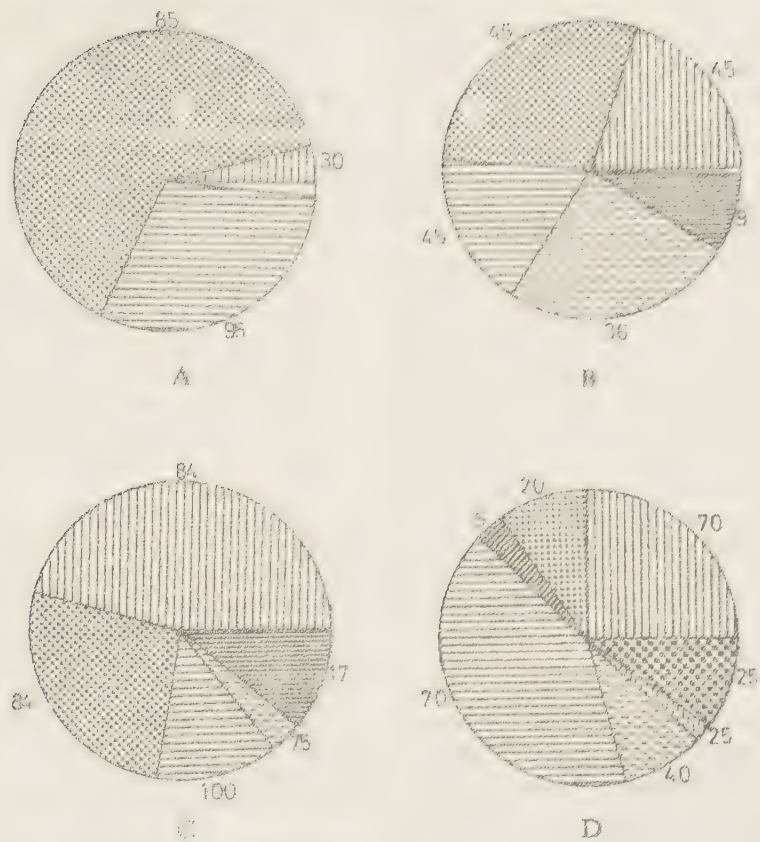


Fig. 5. Composition of the diet of Tufted Ducks (*Aythya fuligula*) shot mainly during the morning flights in 1966/67 in A) September (20 specimens), B) November (11 specimens), C) December (12 specimens), D) March (20 specimens). For further explanation, see Fig. 4.

Tab. 2. Estimated exploitation of the bottom fauna of the Bjärred area by the diving ducks.

Season	Number of bird-day units (Sept.-April)				Total	Bird-days per m ²	Mean consumption, g per m ² , with a consumption of 200 g/bird/day
	<i>Aythya marila</i>	<i>Aythya fuligula</i>	<i>Bucephala clangula</i>	<i>Somateria mollissima</i>			
62-63	2,500	112,000	57,000	100	171,600	0.042	8.4
64-65	16,600	127,000	44,700	300	188,600	0.046	9.2
65-66	21,200	91,000	101,000	200	213,400	0.052	10.4
66-67	15,400	88,400	74,200	100	178,100	0.044	8.7

Food consumption of diving ducks

of the area during the period between the two sampling occasions was 21 tons or $5 \pm 2\%$ of the decrease in total food resources inside the 3 m depth contour. This estimation was based upon the assumption that the 104,000 bird-day units registered during the period consumed 200 g per unit. When the sandbanks are taken as a limit, the percentage will be $9 \pm 3\%$ of the total decrease. As stated above most feeding by the ducks occurred in this latter area. Assuming an (unlikely) food consumption of 300 g/day the figures would be $7 \pm 3\%$ and $13 \pm 4\%$. The estimates of the part of the total decrease in standing crop caused by the feeding diving ducks must be considered as maximum values as some (unknown) production might take place during the period concerned.

In 1965/66 a somewhat different method was used for the quantitative sampling so the values are not fully comparable. The estimated food resources in October were about 600 and 1100 tons respectively with a decrease of 33% by April. The estimated exploitation by the diving ducks during this period was 185,000 bird day units or 37 tons (200 g/bird/day), i.e. 19 and 10% of the decrease in total standing crop of the area inside the sandbanks and the total area inside the 3 m depth contour respectively.

It is not possible to calculate the predation rate on the various food species as the composition of the diet in the Goldeneyes of the area is not known. In the latter species it cannot be excluded that seeds of *Zostera* and

Ruppia have some importance but compared to the other factors influencing the above calculations this effect must be negligible. In the total standing crop all potential food species are included but some are only taken in rather small quantities (crustaceans) and the predation on the most favoured species will certainly be rather heavy, at least locally.

The results above are interesting in relation to Lack's (1968) views of the availability of food in the winter quarters as the factor determining the numbers of migratory bird species. Consequently competition for food between related species should have resulted either in similar species having different winter quarters or having different feeding habits. Differences in food choice (and in feeding places) were also found between the Tufted Duck and the Scaup in the present study, i.e. for an area where the total food resources were sufficient for much larger numbers of ducks than present.

8. Acknowledgements

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Food-seeking activity of south Swedish diving ducks in the non-breeding season

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Aythya marila, *A. fuligula* and *A. ferina* were mainly night-active in coastal areas of southern Sweden except during colder periods when they were partly day-active. On the lakes *A. fuligula* and *A. ferina* showed a higher daytime feeding intensity than at the coast. *Bucephala clangula*, *Clangula hyemalis*, *Somateria mollissima*, *Mergus merganser*, *M. serrator*, and *M. albellus* were day-active. The highest food-seeking intensities were found in the smallest species and in *B. clangula* the smaller females generally had a higher food seeking intensity than the larger males.

B. clangula and *A. fuligula* showed a significant correlation between decreasing temperatures and increased food-seeking intensity. Especially the females of *B. clangula* reached very high food-seeking intensities during the coldest periods and they were then also found to have the areas in larger numbers than the males.

The flights between the resting places and the feeding grounds in both the day-active *B. clangula* and the night-active *A. fuligula* were correlated with sunset and sunrise and occurred at lower light intensities in late autumn and winter compared to early autumn and spring.

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Aythya marila, *A. fuligula* и *A. ferina* в прибрежной зоне южной Швеции, большей частью активны ночью, за исключением холодных сезонов, когда у них наблюдается дневная активность. В озерах *A. fuligula* и *A. ferina* имеют более высокую дневную активность питания, чем на морском побережье. *Bucephala clangula*, *Clangula hyemalis*, *Somateria mollissima*, *Mergus merganser*, *M. serrator*, *M. albellus* активны днем. Наиболее высокая активность поисков пищи зарегистрирована у самых мелких видов, а у *B. clangula* более мелкие самки более активны, чем крупные самцы.

У *B. clangula* и *A. fuligula* установлена определенная корреляция между понижением температуры и увеличением активности поисков пищи. Особенно высока эта активность у самок *B. clangula* в холодные периоды. Установлено также, что самки мигрируют в большем количестве, чем самцы. Время полетов между местом отдыха и местом кормления у дневного вида *B. clangula* и ночного *A. fuligula* коррелирует со временем восхода и захода солнца и наблюдается поздней осенью и зимой при более низкой освещенности, чем в начале осени и весной.

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1. Introduction

Several studies have been published on the feeding habits and change between night and day activity in diving ducks (e.g. Balat 1967, Hansson 1966, Hein 1966, Haugen 1966, Schoenagel 1963, Tamásier 1966). There is only one paper (Klima 1966), a few shorter communications and scattered observations have been published on the activity of diving ducks.

According to some authors food is regarded as the most important regulatory factor for bird populations (Lack 1954). Difficulties in obtaining enough food might be shown by the food seeking intensity, the food seeking activity was included as a part of a study of the non-breeding ecology of diving ducks in south Sweden. The field work was undertaken during September–April 1964/65–1966/67 and 1969.

2. Study areas

Observations were made in two coastal areas and at the inland lakes in southern Sweden (Fig. 1) the most important characteristics of which will be given here. The two coastal study areas, The Sound (Öresund) between Vikhög and Klagshamn (N and S of Malmö) and the south coast of Scania between Ystad and Kåmplinge, are both characterized of extensive shallow areas suitable for feeding diving ducks. Both areas are usually free of ice in the winter, but they have been partly frozen in shorter periods in the winters studied.

The inland lakes are all situated in the southwest of Scania, except Lake Ringsjön in central Scania, studied in 1969. All lakes are quite open and shallow and belong to the eutrophic type.

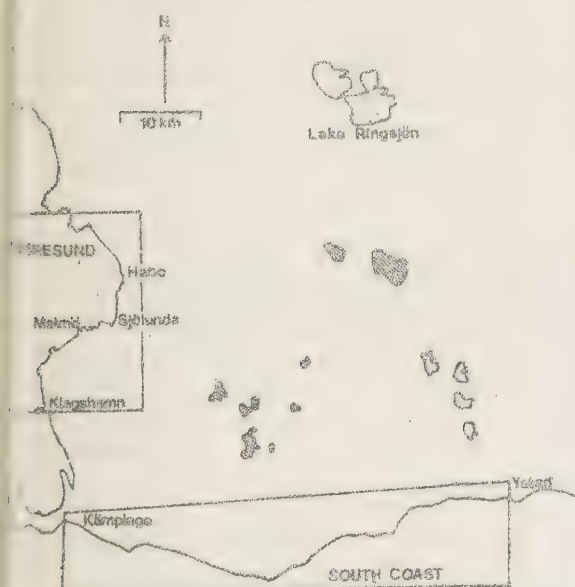


Fig. 1. Map of southwestern Sweden showing the geographical position of the study areas. The lakes studied in 1965 and 1966 are hatched.

3. Methods

The daily activity of the different species was noted in form of standard observations, i.e. a bird or group of birds was followed for a standard period of time and the activity type for each individual was noted (Gibb 1954). As almost all dives in the study areas were of shorter duration than 30 secs. the activity was followed for that period; for the Long-tailed Duck, *Clangula hyemalis* (L.), longer periods had to be used. Only the food-seeking activity is considered here and will be given as per cent individuals food-seeking out of the total observed. A difference between two percentages is considered to be significant when it exceeds three times the standard error of difference between the two values. For days with more than 100 standard observations the relationships between daily mean temperatures for the coastal study areas and the food-seeking intensity of the different species was examined using ordinary correlation and regression analysis. The correlation and regression coefficients were tested with t-test.

The changes between day and night activity were followed in the Tufted Duck, *Aythya fuligula* (L.), and Goldeneye, *Bucephala clangula* (L.), in The Sound area by repeated standard observations on the feeding grounds and observations on the time of arrival and departure of flocks at resting places. The time when 50% of the ducks had departed or arrived or changed activity either from resting to feeding or vice versa was taken as the time of change-over.

4. The activity of the species investigated

4.1. Scaup, *Aythya marila* (L.)

The Scaups are generally associated with Tufted Ducks and occur mainly in The Sound area in one flock that rests on a certain pond when it is free of ice and on the sea when the pond is frozen. The Scaups show the same activity pattern as the Tufted Ducks being mainly night-active (Tab. 1) making regular feeding flights to the sea in the evening and returning at dawn, that is

Tab. 1. Food seeking intensity (as per cent of daytime standard observations) of Scaups, *Aythya marila*, at two types of localities in the Öresund study area in 1964/65 and 1965/66. Number of standard observations in brackets. -- = no observations. The differences between 1965 and 1966 for February and March 1–15 are significant.

Month	1964/65		1965/66	
	Pond	Sea	Pond	Sea
October	0 (66)	—	0 (43)	—
November	2 (115)	—	0 (225)	0 (140)
December	1 (307)	—	—	2 (700)
January	0 (81)	0 (665)	—	2 (1382)
February	—	0 (558)	—	51 (339)
March 1–15	—	28 (637)	—	44 (195)
March 16–31	—	8 (801)	0 (717)	—
April	5 (938)	22 (467)	9 (1028)	—
May	11 (377)	—	7 (42)	—

Tab. 2. Food seeking intensity (as per cent of daytime standard observations) of Tufted Duck, *Aythya fuligula*, at two localities in the Öresund study area in 1964/65–1966/67. Number of standard observations in brackets. — = no observations. — or | between two values denote significant differences. February and March in 1966 had significantly higher food seeking intensity than the other two years except for March 1–15 1967.

Month	1964/65		1965/66		1966/67	
	Pond	Sea	Pond	Sea	Pond	Sea
September	—	—	6 (1119)	—	3 (378)	—
October	3 (2898)	5 (383)	2 (2272)	5 (377)	0 (9013)	—17 (1033)
November	1 (3474)	—	2 (11866)	5 (8465)	1 (10929)	— 6 (4338)
December	2 (3906)	6 (418)	—	3 (13111)	0 (4440)	— 6 (2866)
January	0 (6236)	3 (5831)	—	10 (20767)	—	6 (10280)
February	0 (1900)	8 (2424)	—	32 (15826)	—	9 (6474)
March 1–15	—	12 (12387)	16 (209)	—29 (3115)	6 (749)	—38 (206)
March 16–31	14 (1374)	—24 (2547)	4 (1552)	—32 (1873)	11 (169)	21 (62)
April	7 (3049)	—53 (301)	14 (1746)	—39 (331)	—	—

simultaneously with the flights of the Tufted Ducks. During ice-periods in the winter, when remaining at sea all day, the Scaups showed an increased food-seeking activity during day but it did not show any correlation with the daily mean temperatures of the study area.

4.2. Tufted Duck, *Aythya fuligula* (L.)

The Tufted Ducks are generally night-active in the two coastal study areas and spend the day at special resting places. Only a few individuals were seen feeding in daytime except in spring and during cold periods in the winter, when they were forced to leave their preferred resting places by ice and mainly had to stay on the feeding grounds all day. This was especially the case in February 1966. The proportion of day-active Tufted Ducks was higher on the south coast than in The Sound study area (Tab. 2 and 3) probably because The Sound area had better resting places than the south coast where the Tufted Ducks often stayed near the feeding places all day. In many areas on the Baltic coast

most Tufted Ducks seem to be day-active. On the south coast the intensity of diving in daytime was correlated with the daily mean temperature (Fig. 2).

The evening flights and morning arrivals of the Tufted Ducks were studied at two ponds (at Habo) in The Sound study area in 1965/66 and 1966/67 with complementary observations at some other resting places (Tab. 5). The mean departure for six clear evenings in early autumn was 40 min. after sunset and for six overcast evenings 31 min. after sunset. In late autumn all evenings were overcast and in spring no difference

Tab. 3. Food seeking intensity (as per cent of daytime standard observations) of Tufted Duck, *Aythya fuligula*, in the south coast study area in 1964/65–1966/67. Number of standard observations in brackets. — = no observations. — or | between two values denote significant differences.

Month	1964/65	1965/66	1966/67
November...	10 (62)	— 8 (423)	10 (515)
December...	—	8 (1744)	13 (782)
January.....	5 (490)	— 34 (3021)	— 9 (1176)
February....	10 (703)	— 57 (4833)	— 13 (939)
March.....	24 (1230)	— 46 (1646)	— 13 (102)
April.....	38 (170)	6 (112)	—

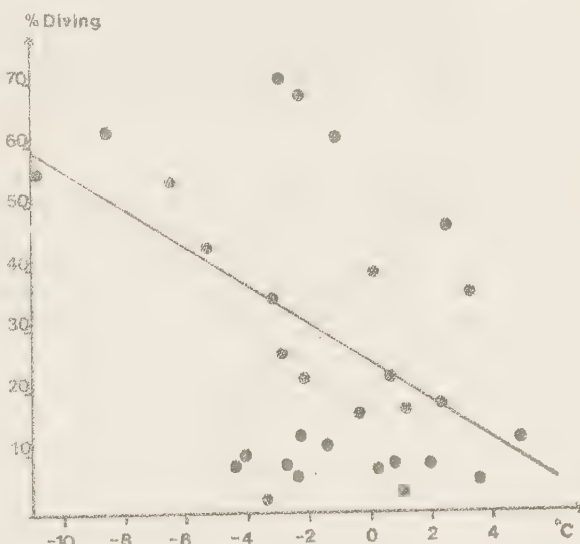


Fig. 2. Feeding intensity (% diving) of Tufted Ducks, *Aythya fuligula*, in the south coast study area in relation to daily mean temperature at Ystad. Only days with more than 100 standard observations were used. Correlation coefficient -0.42 ($0.05 > P > 0.02$). Regression coefficient -2.6 .

4. Food-seeking intensity (as per cent of daytime standard observations) of diving ducks on different lakes in south-Sweden 1965 and 1966 and on Lake Ringsjön in 1969. Number of standard observations in brackets. -- = no observations.

Study year	<i>Aythya fuligula</i>	<i>Aythya ferina</i>	<i>Bucephala clangula</i>	<i>Mergus merganser</i>	<i>Mergus albellus</i>
October 1965	44 (356)	49 (142)	78 (153)	16 (504)	24 (118)
April 1966	60 (448)	64 (200)	75 (208)	35 (558)	—
October 1966	51 (450)	48 (58)	83 (450)	—	—
April 1965	31 (124)	17 (235)	48 (100)	39 (177)	—
October 1969	29 (2052)	28 (764)	83 (614)	—	—
April 1969	39 (1682)	22 (946)	89 (1595)	—	—
October 1969	22 (1490)	0 (297)	94 (1489)	—	—

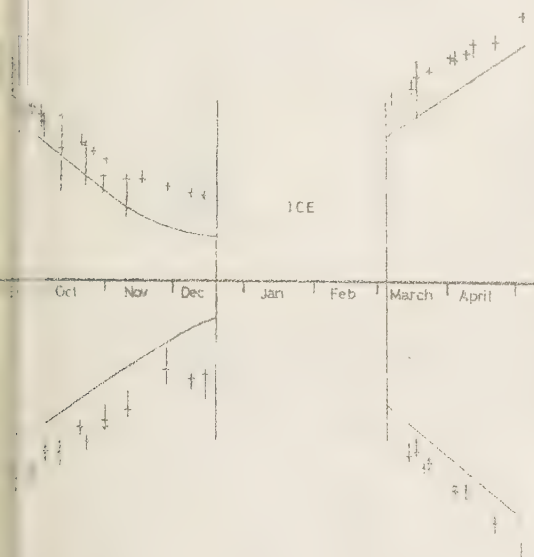


Fig. 1. The timing of evening and morning flights of the Tufted Duck, *Aythya fuligula*, at the Habo ponds, Öresund, Sweden, in 1965/66 and 1966/67. Vertical lines mark the total period of flight, and horizontal bars the time when the ducks left or arrived. Arrows indicate that part of the flight could not be followed. The whole drawn curves show the time for sunset and sunrise.

between overcast and clear evenings could be found. Light intensity at the departure and arrival was generally below 1 lux and the flights seem to be correlated with sunset and sunrise all through the season (Fig. 3). In late autumn the Tufted Ducks left later in relation to sunset and arrived back earlier in relation to sunrise compared to early in the autumn. The greater concentration of evening flights in late autumn and in spring may be noted (Fig. 4). The time sequence of the evening flights varied somewhat between the different localities but was in general the same (Fig. 4, Tab. 5).

On the inland lakes a large proportion of the Tufted Ducks were active in daytime in spring, whereas about 30% of the standard observations in the autumn referred to feeding Tufted Ducks (Tab. 4). No regular feeding flights were seen in Lake Ringsjön but a general dispersion over the lake from the resting places was noted at dusk.

The flight pattern of the Tufted Duck is the same as in other night-active ducks, e.g. Mallard, *Anas platyrhynchos* L., (Hansson 1966, Schoenagel 1963) and Teal, *Anas crecca* L., (Tamasier 1966). These species also showed a relatively later departure and earlier arrival during the shorter days of late autumn.

Table 1. Time of departure and arrival in relation to sunset and sunrise for the feeding flights of the Tufted Duck, *Aythya fuligula*, in The Sound study area in 1965/66 and 1966/67. The time when 50% of the ducks had departed or arrived is used in the calculations.

Locality (Fig. 1)	Period	Time of departure Min. after sunset			Time of arrival Min. before sunrise		
		Mean	S. D.	N	Mean	S. D.	N
Habo ponds (F)	Sept.—Oct. 15	33.7	10.2	13	45.0	9.6	6
	Oct. 15—Dec. 15	43.4	10.3	10	55.0	10.6	6
	March—April	38.7	7.9	12	38.2	4.8	8
Lake Mälaren (L)	Oct. 15—Dec. 15	66.1	7.4	6	—	—	—
	January	61.5	—	2	18.0	—	1
Lake Vänern (K)	Sept.—Oct. 15	43.5	—	2	—	—	—
	Oct. 15—Dec. 15	62.3	10.5	3	—	—	—
	March	41.0	—	1	—	—	—
Lake Mälaren (M)	January	43.5	—	2	—	—	—
Harbour (M)	November	47.5	—	2	—	—	—
Lake Vänern (V)	Sept.—Oct. 15	52.5	—	2	—	—	—
	Oct. 15—Dec. 15	62.8	11.4	5	—	—	—
	January	74	—	1	—	—	—
	April	39	—	1	—	—	—

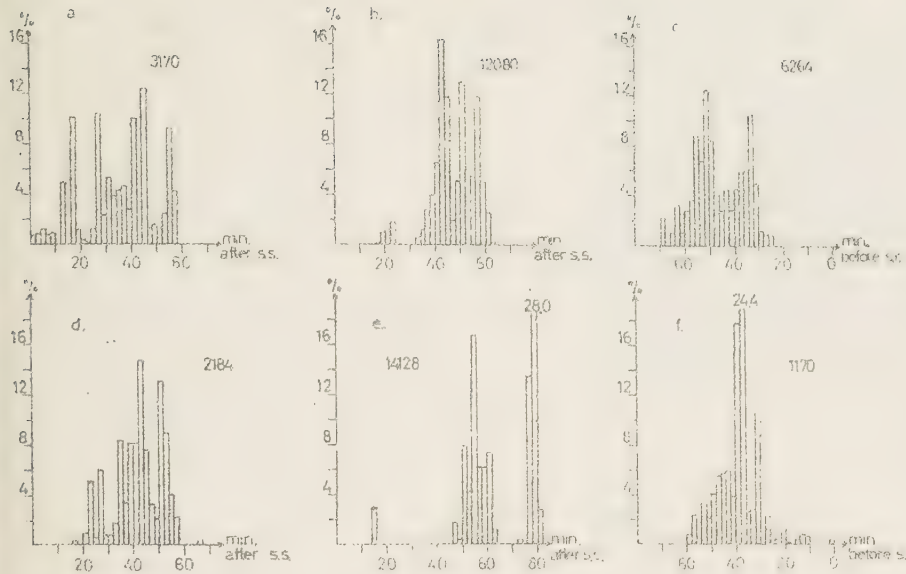


Fig. 4. The time sequence of evening and morning flights of the Tufted Duck, *Aythya fuligula*, at various localities in The Sund study area in 1965/66 and 1966/67. Totals (as per cent of all individuals observed = the figures in each histogram) of leaving and arriving Tufted Ducks at consecutive 2-min. intervals in relation to sunset and sunrise. a) Habo ponds September 1-October 15, b) Habo ponds October 15-December 15, c) Habo ponds arrival in autumn except December, d) Habo ponds in spring, e) Klags-hamn pond, f) Habo ponds arrival in spring.

Tab. 6. Food seeking intensity (as per cent of daytime standard observations) of Pochard, *Aythya ferina*, in The Sound study area in 1964/65-1966-67. Number of standard observations in brackets. — no observations.

Month	1964/65	1965/66	1966/67
September	—	13 (172)	—
October	15 (297)	18 (66)	3 (174)
November	11 (143)	14 (357)	—
December	12 (199)	6 (110)	—
January	4 (53)	20 (133)	—
February	—	51 (63)	—
March	36 (135)	13 (30)	—
April	43 (63)	—	—

4.3. Pochard, *Aythya ferina* (L.)

The Pochard had the same general activity type as the Scaup and the Tufted Duck and in the coastal study

areas they occurred mainly together with the Tufted Ducks making regular feeding flights to sea together with them. The Pochards in the Öresund area generally showed a somewhat higher percentage of day-active individuals than the Tufted Ducks (Tab. 6) but on inland lakes no significant differences were found (Tab. 4).

In central Europe Klima (1966) found no significant differences in food-seeking intensity between day and night during spring. In winter a large proportion were found to be night-active (Bauer and Blotzheim 1969).

4.4. Goldeneye, *Bucephala clangula* (L.)

The Goldeneye is a day-active species with most individuals actively feeding all day (Tabs. 4 and 7). The feeding intensity was always high and showed the highest

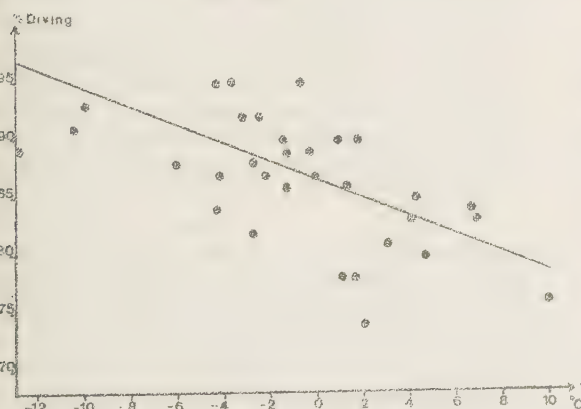


Fig. 5. Feeding intensity (% diving) of female Goldeneyes, *Bucephala clangula*, in The Sound study area in relation to daily mean temperature at Malmö. Only days with more than 100 standard observations were used. Correlation coefficient -0.57 ($P < 0.001$), regression coefficient -0.70 .

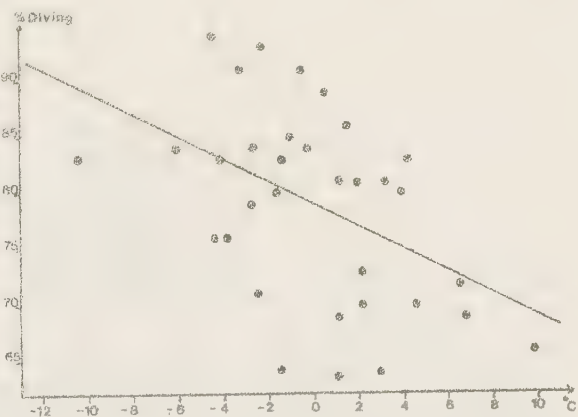


Fig. 6. Feeding intensity (% diving) of male Goldeneyes, *Bucephala clangula*, in The Sund study area in relation to daily mean temperature at Malmö. Only days with more than 100 standard observations were used. Correlation coefficient -0.46 ($P < 0.01$). Regression coefficient -0.97 .

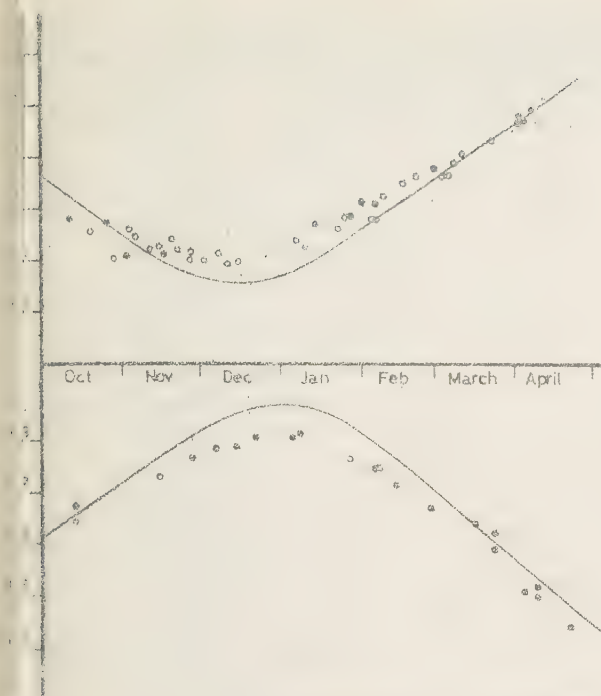


Fig. 7. The start and end of activity in the Goldeneye, *Bucephala clangula*, in The Sound study area as the time when 50% of the Goldeneyes changed activity on the feeding grounds (filled circles) or when 50% arrived or left the resting place (unfilled circles). The whole drawn lines show the time for sunset and sunrise.

values in the coldest months. In most months the females showed a consistently higher feeding intensity than the males in The Sound study area, whereas no differences were found between the sexes in the south coast area. No differences were found in food-seeking intensity between inland waters and the coast. Some differences were found between the south coast and The Sound study area. In six months the males on the south coast had a significantly higher feeding intensity than the males in The Sound study area whereas the females on the south coast had a higher feeding intensity than the females in The Sound area in two months and a lower feeding intensity in four months.

The feeding intensity in The Sound area showed a marked correlation with the mean temperatures of the area reaching high diving intensities during the coldest periods (Figs. 5-6), whereas no such correlation was found on the south coast.

No change in activity during the day could be found. The start and end of daytime activity were studied in The Sound area and was found to be correlated with sunset and sunrise (Fig. 7). A small change in the times of the evening flights in relation to sun was found, the flights occurring relatively later during the short days in November-December than in February-March (Fig. 8). These changes in relation to sun were however small and in no ways compensated for the shorter days or greater food requirements. The Goldeneyes

partly compensated the shorter days in December with a higher feeding intensity and the females in The Sound study area used 90% of their 24-hour activity period in December for food-seeking and 78% of their 12-hour day in March (cf. also Tab. 7).

On the inland lakes the daytime activity generally ended about sunset when the majority of the Goldeneyes gathered in flocks to rest. A few feeding Goldeneyes were generally seen until it was too dark to continue observations. On one occasion in late November more than 50% of the Goldeneyes were still feeding when darkness made observations impossible. In the mornings the Goldeneyes were generally active as soon as it was light.

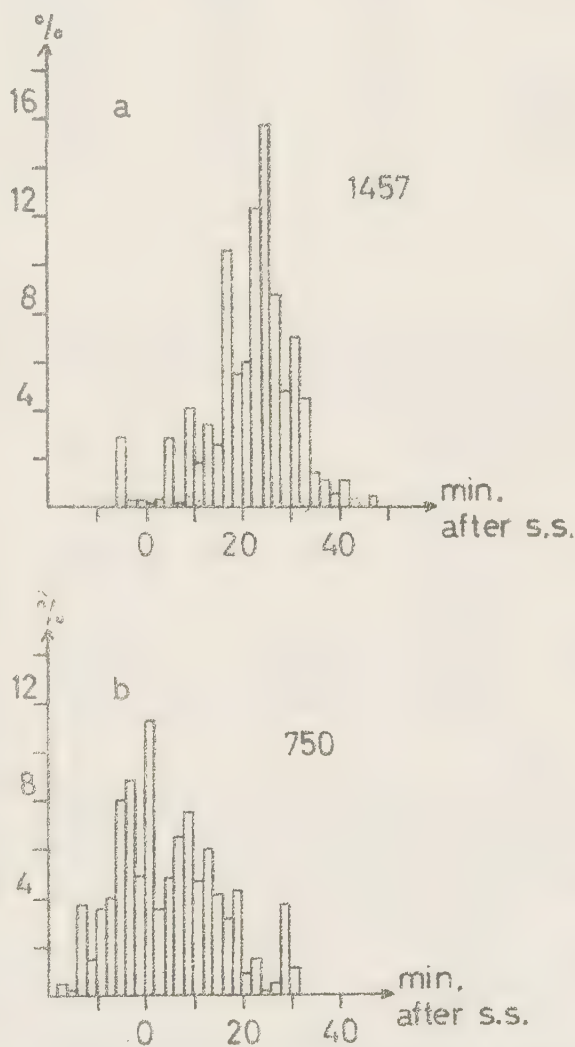


Fig. 8. The time sequence of evening flights of the Goldeneye, *Bucephala clangula*, in The Sound study area. Totals for consecutive 2-min. periods after sunset as per cent of the total number of individuals counted (the number in each histogram). a) November-December (median 24 min. after sunset), b) February-March (median 4 min. after sunset).

Tab. 7. Food seeking intensity (as per cent of daytime standard observations) of Goldeneye, *Bucephala clangula*, in the coastal study areas in 1964/65-1966/67. Number of standard observations in brackets. - = no observations. — or | between two values denote significant differences and * mark values showing significant differences between the two areas.

Year	Month	Tbe Sound		The south coast	
		Females	Males	Females	Males
64/65	October.....	96 (140)	—	—	—
	November.....	77 (239)	58 (89)	84 (95)	—
	December.....	*91 (392)	88 (143)	*78 (328)	— 91 (363)
	January.....	*83 (1403)	— *64 (639)	*73 (1036)	— *77 (1010)
	February.....	*85 (1641)	— 77 (1016)	*75 (869)	75 (615)
	March.....	*76 (2328)	— *68 (1788)	*81 (1533)	*79 (1070)
	April.....	*77 (758)	76 (357)	*69 (343)	70 (92)
65/66	October.....	68 (98)	—	—	—
	November.....	78 (1463)	— 61 (388)	73 (318)	— 58 (212)
	December.....	92 (957)	— 81 (373)	85 (805)	83 (724)
	January.....	89 (1944)	— *55 (1054)	93 (1654)	*92 (1576)
	February.....	90 (1052)	— 85 (953)	88 (1972)	— 81 (1853)
	March.....	*78 (2693)	— *71 (1828)	*86 (1548)	*85 (964)
	April.....	79 (1169)	— 69 (680)	87 (193)	—
66/67	October.....	82 (296)	—	—	—
	November.....	88 (2695)	87 (414)	93 (470)	89 (275)
	December.....	94 (714)	— *73 (308)	92 (599)	*92 (507)
	January.....	94 (1062)	— *84 (418)	94 (876)	*97 (711)
	February.....	89 (1110)	85 (562)	93 (825)	91 (698)
	March.....	82 (983)	— 70 (594)	86 (255)	78 (160)
Mean	December-February.....	90	77	86	87
	March-April.....	78	71	82	78

The pre-dusk gathering of Goldeneyes to special resting places have been described by Breckenridge (1953), King (1961) and Linsell (1969). Sometimes Goldeneyes are active at night (cf. Bauer and Blotzheim 1969, Linsell 1969).

4.5. Long-tailed Duck, *Clangula hyemalis* (L.)

The Long-tailed Duck has the same activity type as the Goldeneye with a high diving intensity throughout the day (Tab. 8). The highest values were found during the coldest months.

Tab. 8. Food seeking intensity (as per cent of daytime standard observations) of Long-tailed Ducks, *Clangula hyemalis*, in the south coast study area in 1964/65-1966/67. Number of observations in brackets. - = no observations. — or | between two values denote significant differences. January and February 1967 differ significantly from the other years.

Month	1964/65	1965/66	1966/67
November....	—	68 (197)	—
December....	69 (306)	73 (991)	83 (134)
January.....	71 (1100)	72 (906)	92 (395)
February.....	80 (1622)	83 (1562)	— 92 (435)
March.....	76 (2102)	— 84 (2218)	—

4.6. Eider, *Somateria mollissima* (L.)

The Eider had a lower feeding intensity than the other day-active bottom feeding species (Tab. 9) with the highest feeding intensities during the coldest months.

Tab. 9. Food seeking intensity (as per cent of daytime standard observations) of Eider, *Somateria mollissima*, in the two coastal study areas in 1964/65-1966/67. Number of standard observations in brackets. - = no observations. — or | between two values denote significant differences.

Month	1964/65	1965/66	1966/67
September.....	—	40 (85)	—
October.....	—	19 (172)	—
November.....	—	25 (611)	— 53 (192)
December.....	—	21 (582)	—
January.....	28 (114)	42 (313)	47 (69)
February.....	58 (55)	42 (310)	50 (81)
March.....	36 (245)	— 49 (346)	—
April.....	13 (237)	— 55 (157)	—

Tab. 10. Food seeking intensity (as per cent of daytime standard observations) of Red-breasted Merganser, *Mergus serrator*, in the south coast study area in 1964/65-1966/67. Number of standard observations in brackets. - = no observations. — or | between two values denote significant differences.

Month	1964/65	1965/66	1966/67
November.....	—	59 (130)	— 77 (328)
December.....	54 (63)	43 (372)	53 (138)
January.....	34 (187)	— 60 (234)	60 (203)
February.....	33 (200)	— 48 (260)	— 35 (239)
March.....	43 (399)	50 (270)	51 (112)
April.....	32 (111)	37 (228)	—

4. Red-breasted Merganser, *Mergus serrator* L.

Observations on daytime activity were obtained from the south coast study area showing a moderately high feeding intensity (Tab. 10). It was high during January and February 1966 when parts of the area were ice-covered. No correlation was found between feeding intensity and mean temperatures. The start and end of activity could not be followed. In spring the Red-breasted Mergansers are generally inactive, gathering at communal resting places at dusk and leaving them before dawn (Nilsson 1965).

5. Goosander, *Mergus merganser* L.

Goosander is day-active but had a markedly lower feeding intensity than its smaller relative, probably related to the different sizes of the prey taken (Tab. 11). In the Red-breasted Merganser some variation occurred between different months. In the hard winter of 1965/66 the feeding intensity during the coldest month (February) was higher than in the two milder winters. No correlation was however found between feeding intensity and daily mean temperatures.

Tab. 11. Food seeking intensity (as per cent of daytime standard observations) of Goosander, *Mergus merganser*, in the two coastal study areas in 1964/65-1966/67. Number of standard observations in brackets. - = no observations. — or | denote significant differences. January 1965 and 1967 show significantly different values.

Month	1964/65	1965/66	1966/67
November.....	—	25 (143)	—
December.....	—	18 (435)	15 (144)
January.....	16 (236)	21 (2079)	25 (538)
February.....	7 (1068)	— 28 (1934) —	15 (631)
March.....	12 (1298)	19 (378)	9 (110)
April.....	—	38 (145)	—

The feeding intensity on the inland localities was similar to the recordings from the coastal areas (Tab. 4). The start and end of activity could not be exactly determined but in general the Goosanders started fishing rather late in the morning and the fishing ended well before sunset.

6. Smew, *Mergus albellus* L.

The Smeews are day-active as the other mergansers and had a similar feeding intensity in the different months as the Red-breasted Mergansers (Tab. 12). The start and end of activity could not be established for the Smew, but on one occasion when unusually many Smeews were present in Malmö harbour in The Sound area they undertook an evening flight to a resting place in another part of the harbour at sunset.

Tab. 12. Food seeking intensity (as per cent of daytime standard observations) of Smew, *Mergus albellus*, in The Sound study area. 1963, 1965 and 1965/66. Number of standard observations in brackets. - = no observations.

Month	1962/63	1964/65	1965/66
November.....	—	—	62 (52)
December.....	—	—	45 (82)
January.....	46 (39)	40 (65)	56 (46)
February.....	64 (50)	35 (57)	46 (63)
March.....	51 (83)	41 (85)	20 (46)

5. Discussion

The diving ducks may be placed into two different groups: those mainly feeding at night: i.e. Scaup, Tufted Duck and Pochard and those mainly feeding in daytime, i.e. the rest of the species studied. However the night-active species are not always strictly night-active and some regional differences occur. In spring on inland waters they feed both day and night with resting periods in between. Moreover the Tufted Ducks were found to be mainly day-active in areas in the Baltic. On the other hand both Tufted Ducks and Pochards show the same activity type on many localities in the Netherlands as they do in southern Sweden (personal observations). The day-active species on the other hand show the same activity type everywhere.

The Scaups and Tufted Ducks are mollusc feeders in coastal waters and will thus have no difficulties in feeding at night (Nilsson in prep.). The same applies to Tufted Ducks on the inland waters which feed mainly on chironomid larvae and the Pochard which takes chironomid larvae and vegetative food (Nilsson in prep.). Among the day-active species the Eider is also a definite mollusc feeder, whereas the Goldeneye and Long-tailed Duck while mainly feeding on molluscs also take quantities of more motile animals such as crustaceans (Nilsson in prep.). The mergansers finally are fish-eaters (Bauer and Blotzheim 1969). In the mergansers, Long-tailed Duck and Goldeneye the motile prey will probably make it necessary for them to feed by day. The Eider, however, could also feed by night. It must be noted that it cannot be excluded that the day-active species occasionally feed also at night. Stomachs of day-active species collected in the early morning were however generally found to be empty. The only species shown to be almost exclusively day-active were the Goldeneye and Goosander and even in these species it cannot be excluded that some left the night-places for feeding and returned again during the night. It was only possible to check the night places in the evening and morning.

The nocturnal feeding in the Scaup, Tufted Duck and Pochard may at least partly be a response to disturbance on the feeding grounds. Especially the Tufted Duck generally occurs in areas with regular disturbance from small boats in daytime. Similarly the nocturnal feeding flights of many surface feeding ducks (*Anas* spp.) is

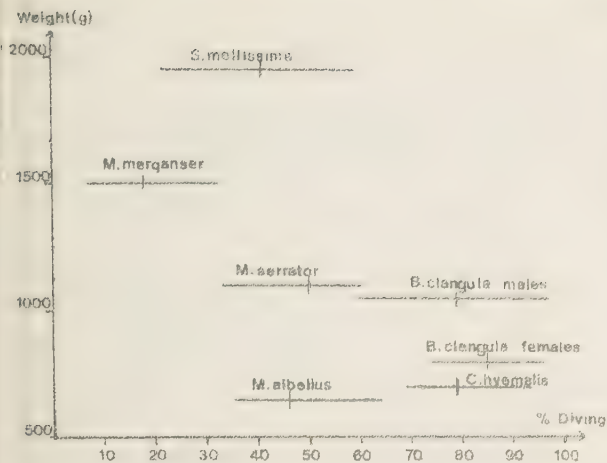


Fig. 9. Feeding intensity (% diving) in day-active diving ducks during November–March in relation to general body weight (according to Bauer and Blotzheim 1969). The horizontal lines indicate the spread of the monthly values and the vertical bars the means of these values.

probably largely related to extensive shooting and other kinds of disturbance (Hochbaum 1960). The other species, feeding at least partly on motile prey, cannot evade disturbance by being night-active. Moreover both the Goldeneye and Long-tailed Duck are better flyers than the Scaup and Tufted Duck and can thus easier evade disturbances.

The various day-active species differ in food-seeking intensity (Fig. 9). For species feeding on the same kind of food the larger species generally showed a lower feeding intensity compared to the smaller species, as could be expected. The Long-tailed Duck, however, showed a slightly lower food-seeking intensity than the somewhat larger Goldeneye, but it is a more efficient diver (Nilsson in prep.).

One of the two species showing the highest feeding intensities, the Goldeneye, also showed a significant correlation between feeding intensity and mean temperature in The Sound study area. Particularly the smaller females showed high feeding intensities during the coldest periods. The night-active Tufted Duck and Scaup responded to colder weather by continuing to feed in daytime. In the other species the highest feeding intensities were found in the coldest months but no correlation was found between feeding intensity and the mean temperature.

Nilsson (1969) found that the food supplies were sufficient for the diving ducks in an area in The Sound study area, and the situation is probably the same in other parts of the coasts of south Sweden (Nilsson in prep.). Still for a day-active species such as the Goldeneye the food situation might be highly critical during the coldest periods in the winter since even during nor-

mal periods they spend a large part of the short days seeking food and are thus unable to extend this appreciably when requirements increase. The situation is often accentuated as the shallow areas become covered with ice and the birds have to feed in deeper water taking more time to obtain the same quantity of food. In the Goldeneye the females are smaller than the males and were found to have a higher food seeking intensity. During cold periods there was a shift in sex-ratio in the study areas from female to male dominance as many females left the areas (Nilsson 1970).

The Tufted Duck, although being a less efficient diver, is probably in a better position to obtain sufficient quantities of food during cold periods than the day-active Goldeneye, as it can feed during both day and night if necessary. Some Goldeneyes were found to leave the study area in The Sound temporarily during the periods with heavy ice-coverage, whereas the Tufted Ducks concentrated to the few open areas remaining (Nilsson in prep.). Similarly in January more Tufted Ducks per Goldeneye were seen in the archipelago areas of the Baltic than on the south coast of Scania and other more open coasts. This proportion was also higher on Gotland than on the south coast of Scania and on the German coast, where the highest number of Tufted Ducks per Goldeneye was recorded in the east (Nilsson in prep.).

The feeding flights of waterfowl were discussed by Hein and Haugen (1966) and Hochbaum (1960) and found to be influenced by light and metabolic factors (cf. Aschoff and Wever 1962 for a general discussion on changes in activity). The changes in activity in Tufted Duck and Goldeneye in south Sweden during the winter were also found to be correlated with sunrise and sunset. The relatively earlier and later occurrence of the flights in relation to sunrise and sunset during late autumn and midwinter in both species points to the importance of other factors than light alone. In the Goldeneye the shorter period for feeding in midwinter is probably the main factor while the change in start and end of activity in relation to sunset and sunrise does not compensate for the shorter day (cf. Hein and Haugen 1966). The opposite is true for the Tufted Duck that probably does not need the whole long night for food-seeking.

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Local and Seasonal Variation in Sex-Ratios of Diving Ducks in South Sweden during the Non-Breeding Season

LEIF NILSSON

Nilsson, L. Local and Seasonal Variation in Sex-Ratios of Diving Ducks in South Sweden during the Non-Breeding Season. *Ornis Scand.* 1, 115-128, 1970.

The sex-ratio of diving ducks during the non-breeding season was studied in southernmost Sweden in 1959-69. Differences in sex-ratio between flocks of different sizes and between different parts of a locality were found in *Aythya fuligula* and *Bucephala clangula*. Seasonal variations in sex-ratio were found in all species. Autumn migration was initiated by males in *A. fuligula* and *A. ferina*, and by females and immature birds in *B. clangula*, *Mergus merganser* and *M. albellus*. In all these species males initiated spring migration and dominated over the females in most Swedish winter localities. In *A. marila* the percentage of males increased from autumn to spring, whereas the opposite was found in *Clangula hyemalis*.

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INTRODUCTION

Sex-ratios are important in the management of waterfowl and have attracted the attention of many scientists, especially in North America (e. g. Beer 1945, Bellrose et. al. 1961, Dathe 1964, Ericksson 1943, Eygenraam 1957, Johnsgaard & Bass 1956, Linkola 1960, Petrides 1944, Yocom 1949).

In a study of the winter ecology of diving ducks in south Sweden, a large body of data on sex-ratios was obtained, and will here be analysed in terms of different habitat selection and migration patterns between the sexes.

STUDY AREAS

The observations were mainly collected in three areas (two coastal and one inland) in southwest Scania 1962-68 (Fig. 1).

Both of the two coastal areas, Öresund be-

tween Vikhög and Klagsåmn, and the south coast between Ystad and Kämpinge, have large areas of shallow water with good feeding grounds for diving ducks.

The inland area in southwest Scania comprises a series of small to medium-sized eutrophic lakes with varying vegetation. When free of ice, the lakes support large numbers of resting ducks.

Additional sex-ratio data were obtained from the wildfowl counts in Sweden from 1959 to January 1969 (cf. Nilsson 1968a, 1968b).

METHODS

Collecting the data

Standardized mapping tours were made at least twice a month during October-April 1964/65-1966/67. All groups of diving ducks were counted separately, entered on large scale maps,

and supplemented with notes on numbers of each sex and activity of the group. When many small groups were concentrated in one area, only the area was registered on the map, but the groups were still counted and listed separately. In 1962-64 and 1967/68 sex-ratio counts were only made in parts of the study areas.

The observations were made by telescope (40×60) and binoculars (10×50) from fixed observation points, chosen so that the birds in the area between the two points could be adequately counted. Conspicuous landmarks served as borders for the counting sectors. Observations were restricted to favourable weather conditions.

Sources of bias

Sex-ratio counts in ducks are subject to various sources of bias. Some birds may be overlooked, but in the present study the observation points were so situated that there were no risks of coast-bound ducks not being detected. As for

the Long-tailed Duck, *Clangula hyemalis* (L.), which stays far out at sea, only part of its population could be seen from land even under the most favourable weather conditions.

In day-active species, the intensive diving in dense flocks introduced an important source of error, whereas the counts of night-active species were made on resting flocks. Every flock was followed for a while to check the first count. Larger flocks were frightened by a slow approach; it caused the ducks to stop diving and swim slowly away from the shore, thereby offering good opportunities for observation. Errors in counts of individual flocks of moderate size were thus negligible. Large compact flocks of Tufted Duck, *Aythya fuligula* (L.), with more than 1000 individuals were almost impossible to count accurately. Counts are thus lacking for some sectors in this species. In smaller flocks of about 200-800 individuals, a counting error of about 10 % was estimated from repeated counts.

The brilliant winter plumage of the males makes them easier to detect than the duller



Fig. 1. Map of southwest Scania showing the general position of the study areas. The lakes of the lake study area are hatched.

females. Under poor light conditions this may affect the results, but in the present study counts were not made under such conditions.

Finally, the immature males of some species may be difficult to separate from the females, especially in the early autumn. In some species (the Goldeneye, *Bucephala clangula* (L.), and mergansers), first-winter males are similar to the females in the early autumn, but may be separated from December onwards.

Evaluation of data

All sex-ratios are given as percentage of males. Sometimes percentages of adult males will be discussed in relation to females and immature birds.

For the commonest species, only days with counts of more than 100 individuals were used to calculate monthly means of the percentages of males. In all cases the individual values were quite close to the mean and showed no significant deviations. In the Tufted Duck and Goldeneye, the means and standard error for different sectors and areas were calculated for each month over all years to test local variation. A Wilcoxon-Rank Sum test (Dixon & Massey 1957) was used to test differences between sectors with widely different numbers of individuals. Seasonal trends were tested with correlation analysis.

In the rarer species, these methods could not be applied, so all counts in one month were added together to obtain a monthly value (weighed mean). When no differences were found between the same months in different years, the values were added in the tables. In the same way, the data from the wildfowl counts included many counts which were too low and heterogeneous to be tested statistically, and were accordingly added together when not showing any significant differences (i.e. difference less than standard error). The complete data from wildfowl counts will thus only give a general idea of the sex-ratio in the parts of the country concerned. In general, however, only small variations were found between different localities.

SEX-RATIOS OF THE SPECIES INVESTIGATED

Scaup, *Aythya marila* (L.)

Counts were obtained from Lommabukten, where a flock of several hundred individuals stayed during the winter season (Fig. 2). The Scaups mainly appeared together with the Tufted Ducks, but showed a quite different seasonal variation in the sex-ratio, with a marked dominance of females during the early autumn and an increasing proportion of males during the winter, coinciding with the increase in the number of resting Scaups in the area. This pattern was not found in any other species.

Tufted Duck, *Aythya fuligula* (L.)

The Tufted Duck is night-active with special resting places (often ponds), where compact flocks of up to several thousand individuals can be observed, and from which regular feeding flights to the sea are performed. Marked differences in sex-ratio were found between some sub-areas of the Öresund study area and between the Öresund area and the south coast. Those main flocks in the Öresund area that were not counted and the flock at Sjölanda

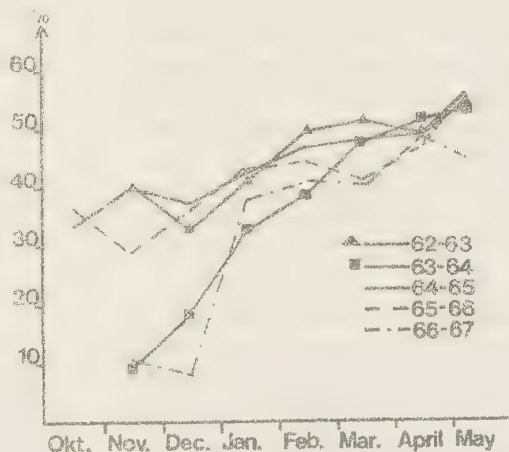


Fig. 2. Percentage of males among Scaups, *Aythya marila*, in the Öresund study area 1962/63–1966/67. Monthly means from counts of all Scaups in the area. Correlation coefficient for all years together is 0.74 ($P < 0.01$).

Table I. Percentage of males among Tufted Ducks, *Aythya fuligula*, in sub-areas of the Öresund study area 1962-67 and the south coast 1964-67. Mean values $\pm$ standard error. Number of counts in brackets. Only days with more than 100 individuals present in the area were used

Month	Habo Pond	Sjölunda Open sea	Sjölunda Inclosed area	Sjölunda Pond	Limhamn	Klagshamn Pond	South coast
Sept.	62.1 $\pm$ 1.2 (16)	—	—	68.8 $\pm$ 2.7 (5)	—	70.3 $\pm$ 2.9 (3)	—
Oct.	55.5 $\pm$ 1.4 (13)	—	62.8 $\pm$ 1.4 (6)	61.9 $\pm$ 3.3 (14)	—	68.3 $\pm$ 5.7 (4)	—
Nov.	59.8 $\pm$ 1.3 (18)	37.5 $\pm$ 2.4 (6)	61.5 $\pm$ 2.0 (10)	60.4 $\pm$ 1.9 (10)	—	61.0 $\pm$ 0.6 (5)	32.3 $\pm$ 7.4 (3)
Dec.	—	49.7 $\pm$ 3.4 (6)	54.3 $\pm$ 2.2 (9)	—	25.3 $\pm$ 3.2 (3)	—	49.8 $\pm$ 2.0 (4)
Jan.	—	53.7 $\pm$ 5.3 (6)	63.5 $\pm$ 1.9 (10)	—	48.6 $\pm$ 3.2 (7)	—	44.6 $\pm$ 1.7 (7)
Feb.	—	56.7 $\pm$ 4.5 (5)	61.6 $\pm$ 3.6 (8)	—	45.3 $\pm$ 4.3 (6)	—	50.9 $\pm$ 2.3 (8)
March	52.9 $\pm$ 2.0 (10)	55.1 $\pm$ 1.1 (8)	47.5 $\pm$ 1.1 (8)	51.7 $\pm$ 1.7 (6)	42.8 $\pm$ 1.3 (4)	54.8 $\pm$ 1.7 (4)	51.9 $\pm$ 2.2 (8)
April	59.8 $\pm$ 0.8 (18)	—	—	60.0 $\pm$ 1.8 (12)	—	57.3 $\pm$ 1.3 (10)	63.6 $\pm$ 2.7 (5)

Table II. Percentage of males in flocks of different sizes in the Tufted Duck, *Aythya fuligula*, in Malmö harbour during December-February 1964/65 and 1965/66

Size of flock	Males (percent)	Numbers counted	No. of flocks
1-25	33.2	510	39
26-50	33.5	556	16
51-100	47.8	702	9
101-200	46.2	1283	10
201-300	55.0	1742	7
301-	65.2	6192	11

generally showed sex-ratios which were higher than those on the south coast (Table I). Because of the compact flocks in some sectors of the Öresund area, counts could only be made in some sectors here.

The males predominated in areas with large numbers, whereas females often predominated in areas with low numbers and smaller flocks (see Limhamn in Table I). In areas with large resting flocks, smaller flocks often occurred apart from the main flocks. The smaller flocks generally had a lower percentage of males than the large flocks (Table II).

Of the two ponds at Habo, one had only a narrow border of *Phragmites* whereas the other smaller pond, separated from the first by a narrow road bank, was roughly two-thirds covered with *Phragmites*. The smaller pond had a marked predominance of females in the autumn, whereas the males predominated at the larger pond (Table III). In the evening flights, the Tufted Ducks from the two ponds behaved as a single flock; the smaller pond had about one-tenth of the total number.

Sex-ratio counts from inland Scania and from inland Sweden north of Scania showed a lower percentage of males than in Öresund in October-November (Table IV). However, during August and September Lake Ringsjön had a marked predominance of males among moulting and resting Tufted Ducks. During March the inland waters had a higher percentage of males than the coasts of Scania. At Hallsjön, Trollhättan, in south central Sweden, males

Table III. Percentage of males among Tufted Ducks, *Aythya fuligula*, resting on two ponds at Habo, Öresund, based on full counts of all resting individuals

Month and year	No. of comparisons	Pond with <i>Phragmites</i>			Open pond			Probability level
		Mean	Range	Total No. of ducks	Mean	Range	Total No. of ducks	
Sept. 63.	2	47	44-50	130	60	58-62	464	—
64	1	31		85	74		517	—
65	5	52	21-68	627	68	62-73	428	P < 0.05
Oct. 63	3	39	32-50	160	61	53-65	746	P < 0.05
64	3	26	21-28	236	62	59-67	1895	P < 0.05
65	2	49	45-53	1105	68	57-79	637	—
Nov. 64	2	16	12-21	86	61	59-63	1214	—
65	4	35	23-38	386	61	60-65	1600	P < 0.05
66	8	22	6-33	1085	64	60-70	9057	P < 0.001

dominated the whole spring migration (Nilsson 1965).

The seasonal variation in the sex-ratio of the Tufted Duck in Sweden is still unclear, but the major features may be deduced. Most of the males seem to leave the breeding areas before the females because of their earlier moult (cf. Bezzel 1964). Since the migration south begins after the moult, a predominance of males is found in some areas on the coasts of south Sweden in early autumn. This leaves females predominating on the breeding and moulting grounds in October. The lower percentage of males on the south coast compared to the Öresund area might be explained by the later arrival of the Tufted Ducks on the south

coast. The ducks mainly arrive here when the inland areas start to freeze, and thus come from areas where the majority of males have already left and which have a higher proportion of females. The reason for the later arrival on the south coast is probably the better resting places in the Öresund than on the south coast.

In spring, migration is initiated by the males, and thus a higher percentage of males was found at inland localities than at the coastal waters.

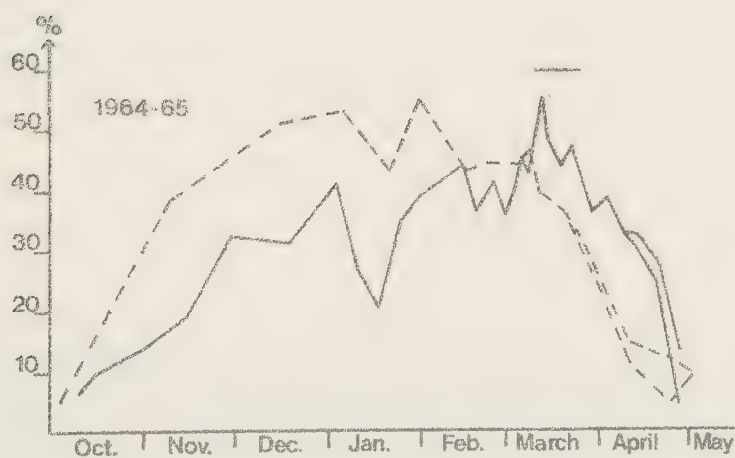
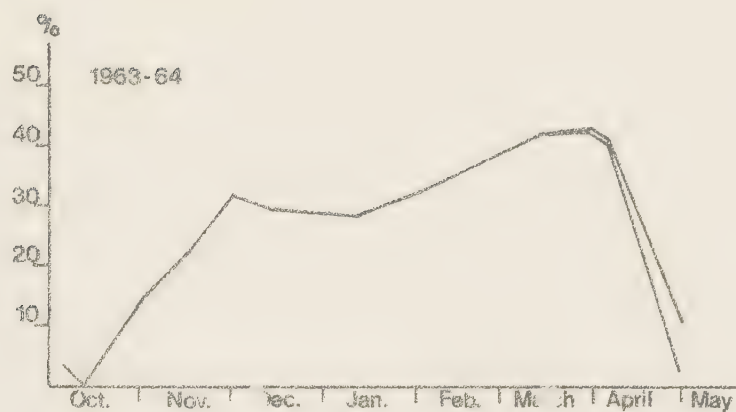
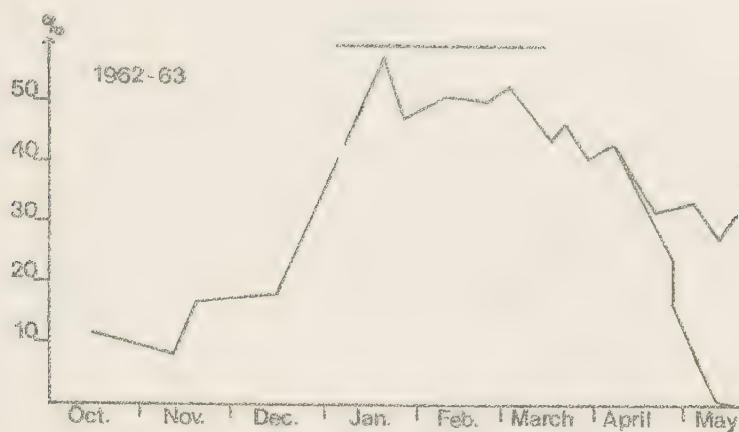
There are only few data on the sex-ratio of the Tufted Duck published. Engström (1961) and Engström & Ehrström (1957) published

Table IV. Percentage of males among Tufted Ducks, *Aythya fuligula*, on inland waters in Sweden 1959/60-1966/67. Numbers counted in brackets

Month	Scania	North of Scania (Wildfowl counts)
Oct.	36.4 (244)	47.2 (735)
Nov.	46.4 (648)	44.6 (411)
Dec.	—	51.6 (477)
Jan.	—	51.3 (480)
Feb.	—	55.8 (640)
March	64.7 (1326)	64.9 (387)
April	59.6 (1866)	58.2 (1666)
May	74.1 (143)	62.4 (708)

Table V. Percentage of males among Pochards, *Aythya ferina*, in SW Scania 1961/62-1968 and at the wildfowl counts in Sweden 1959/60-1966/67. Numbers counted in brackets

Month	SW Scania		Wildfowl counts (excl. Scania)
	Öresund	Inland lakes	
Sept.	70.5 (496)	—	—
Oct.	68.5 (872)	75.6 (697)	61.0 (223)
Nov.	70.5 (939)	76.6 (298)	65.5 (156)
Dec.	76.9 (456)	—	75.0 (56)
Jan.	72.8 (309)	—	77.3 (53)
Feb.	68.1 (545)	—	70.8 (96)
March	67.2 (622)	76.6 (424)	56.3 (64)
April	72.3 (502)	68.9 (710)	73.8 (1502)
May	79.7 (153)	82.2 (56)	74.7 (387)



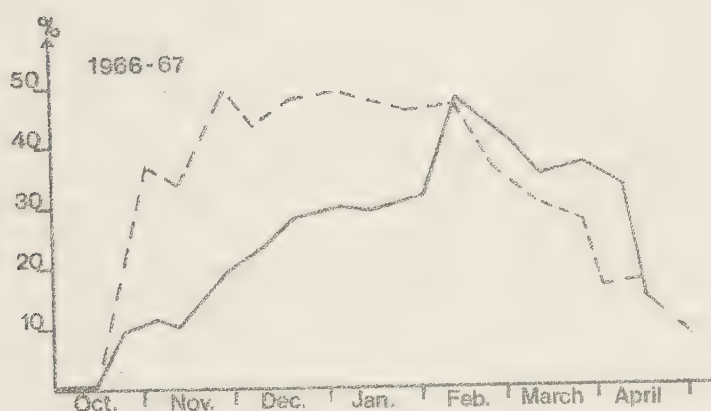
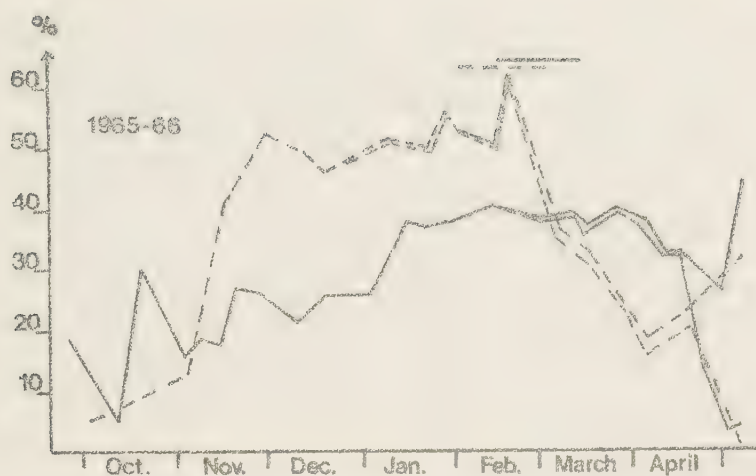


Fig. 3. Percentages of males among Goldeneyes, *Bucephala clangula*, at Lommabukten, Öresund (—) and at the south coast of Scania (-----) in 1962/63–1966/67. All values are from counts of the total number of ducks in the area. Before 1 December first-winter males could not be regularly separated from females, so the curves for this period represent per cent adult males. From 1 December onwards first-winter males could be separated; the upper curve represents total number of males and the lower curve, adult males. Ice periods are marked with horizontal lines.

counts from Stockholm showing only slight deviations from equal sex-ratio. Boase (1926) in Scotland found that females preferred fresh water, whereas most males rested at sea. In Germany (Bezzel 1959, Ehrlich 1963, Dathe & Profft 1936, Frieling 1934), and in Switzerland (Burckhardt 1958), varying degrees of male predominance was found during the winter as in Sweden. The seasonal changes in sex-ratio in southern Germany were similar to those in Sweden (Bezzel l.c.). In spring, sex-ratios among arriving Tufted Ducks in Finland were the same as in Sweden (Hildén 1964, Linkola 1960).

Pochard, *Aythya ferina* (L.)

A marked unbalance in sex-ratio is evident from all counts (Table V, cf. also Nilsson 1965), but the variation in sex-ratio between localities was small.

In southern Germany, males predominated in early autumn, owing to their earlier moult, whereas females arrived later, but males predominated markedly during the winter and left earlier than the majority of the females (Bezzel 1959, cf. also Dathe & Profft 1936, and Frieling 1934). The Swedish data, being rather limited, do not demonstrate any marked seasonal variation, males being markedly predominant in the whole season. In March, the higher sex-ratio on the lakes compared to the coast indicates that males here, as in Germany, initiate spring migration. In Switzerland males predominated in the winter (Burckhardt 1958) and they were also found to dominate spring migration in Finland (Hildén 1964, Linkola 1960).

Goldeneye, *Bucephala clangula* (L.)

In the Goldeneye, first-winter males are very similar to the females during the early season. In October and November discrimination is difficult, so the figures for these months are given as percentage of adult males. From December onwards, discrimination is possible but almost no first-winter males occurred in the study areas from December to early April.

Thus adult males can be considered the same as males' total for this period.

Significant differences in the percentage of males (adult and total) occurred between many sub-areas of the two main study areas on the coasts of Scania and between the two main areas (Fig. 3, Tables VI and VII).

The females and immature birds arrived earlier than the adult males in the autumn. Most immature birds passed on directly, whereas the females stayed and dominated the winter population in the Öresund area. In spring, males departed earlier than the females. Immature ducks arrived even later and constituted a large proportion of the Goldeneyes in late spring in some years. It may be noted that the decrease in the percentage of males in the spring was simultaneous with the spring influx in March. In two seasons, 1964/65 and 1966/67, a marked increase in the percentage of males was noted at the start of spring migration before the decrease.

Marked variation was found from year to year. Lommabukten generally had female dominance during the winter, but the percentage of males increased during cold periods, and in the hard winter of 1963 about 50 % males were recorded during the ice-period.

The south coast generally had a higher percentage of males than the Öresund area, with about 50 % males in January and February. The differences between the years were rather

Table VI. Percentage of adult males among Goldeneyes, *Bucephala clangula*, on the coasts of Scania. Mean values and standard error of the counts from Lommabukten and the south coast shown in Fig. 2. Number of counts in brackets

Month	Lommabukten 1962-67	The South coast 1964-67
Oct.	8.3±2.0 (13)	5.7±0.5 (4)
Nov.	17.5±1.8 (16)	35.5±4.5 (7)
Dec.	24.2±2.4 (8)	40.9±3.4 (5)
Jan.	35.3±2.6 (13)	50.1±1.3 (9)
Feb.	40.9±1.9 (11)	47.7±2.4 (6)
March	42.7±1.1 (20)	34.1±2.1 (10)
April	27.4±2.9 (18)	15.8±2.3 (9)
May 1-15	5.3±1.3 (4)	—

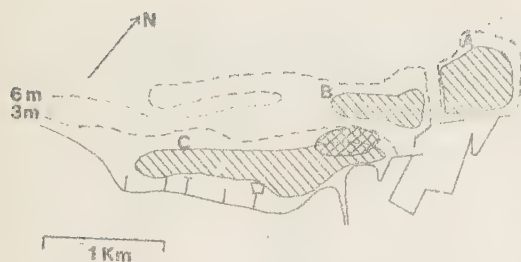


Fig. 4. Map showing the Ribersborg area, Öresund, with feeding grounds (A–C) and the resting place (cross-hatched) of the Goldeneye, *Bucephala clangula*, marked out. Feeding areas A + B comprise the outer sector and C the inner (cf. Table VII).

small. In all years the south coast had a high percentage of males early in the season. In the spring, the Goldeneyes left the south coast earlier than the Öresund area, with males departing in relatively greater numbers in the first exodus. This resulted in a lower percentage of males on the south coast than in the Öresund area in March and April. In the mild winter of 1966/67 the shift was earlier than in the other winters studied. The difference is probably related to the different topography of the two areas: Öresund has extensive shallow areas with favourable feeding grounds, whereas most feeding grounds on the south coast are in deeper water. This might result in a later departure of the Goldeneyes from Öresund, thus causing a higher percentage of males here than on the south coast, where the wintering birds leave early and are replaced by new arrivals from the south. The latter have a higher proportion of females and immature birds.

The percentage of immature ducks varied

from year to year (Fig. 3). In the winter few were seen, but they were common in the spring in some years, especially 1962/63 and 1965/66.

As stated, marked differences in sex-ratio occurred between sub-areas of the main study areas. In some areas this was studied in more detail (see below).

In Fig. 4, the main feeding areas of the Goldeneye at Ribersborg, Malmö, in the Öresund area in 1965/66 and 1966/67 are shown as well as the resting place where all individuals congregated at night. Feeding areas A and B are in deep water (4–6 m), whereas C is in shallow water. All areas have a stony bottom, with a rich fauna dominated by *Mytilus edulis* L. The Goldeneyes were generally more common in the outer sector than in the inner, where only about one-fourth were counted. In all months males were in marked predominance in the outer sector, whereas females dominated the inner (Table VII). Similar results were obtained in some of the other areas.

In some areas with rather deep water on the south coast, the Goldeneyes occurred in larger flocks compared to the smaller groups in the Öresund area, and in some areas with shallow water on the south coast. These flocks generally stayed outside small moraine points with stony bottom and large stones on the shoreline. At many such places, two flocks were seen, one outer-dominated by males and one inner-dominated by females. The percentage of males at one locality was 43.2 % in the inner flock and 66.5% in the outer flock ($P < 0.001$, total numbers counted 697 and 573 respectively) for all counts in one winter.

Table VII. Percentage of males among Goldeneyes, *Bucephala clangula*, in two sectors of the Ribersborg area near Malmö, Öresund in 1965/66 and 1966/67. See Fig. 4!

Month	No. of comparisons	Inner sector		Total No. of ducks	Outer sector		Total No. of ducks	Significance
		Mean	Range		Mean	Range		
Dec.	3	26	22–29	130	70	65–75	238	$P < 0.05$
Jan.	4	32	24–42	291	72	59–78	1048	$P < 0.05$
Feb.	6	38	31–53	382	73	49–81	1240	$P < 0.01$
March	4	36	31–42	287	57	54–62	503	$P < 0.05$

Table VIII. Percentage of males of Goldeneyes, *Bucephala clangula*, in flocks of different sizes on the south coast of Scania in December–February 1964–67. No first-winter males were seen in the period concerned. Numbers counted in brackets

Size of flocks	Percentage of males		
	1964–65	1965–66	1966–67
1–5	46 (753)	49 (350)	41 (507)
6–10	47 (619)	48 (224)	43 (538)
11–20	55 (862)	53 (606)	44 (944)
21–30	48 (663)	60 (386)	53 (599)
31–40	55 (534)	56 (464)	45 (419)
41–60	54 (463)	61 (244)	57 (755)
61–80	53 (206)	65 (414)	49 (352)
81–100	66 (357)	53 (271)	49 (350)
101–	—	64 (220)	65 (685)

The separate distribution of the sexes may indicate different diving skill (Haartman 1945, Mester & Prünke 1966), but studies on Göta älv (Nilsson 1969a) and on the coasts of Scania showed no differences in diving ability between the sexes. On the other hand, differences in food-seeking intensity were found between the sexes, the females showing a higher food-seeking intensity than the males. Thus there is probably a greater need for the females to stay on shallow water where diving is more economic (cf. Nilsson 1970).

Johnsgaard & Bass (1956) found a markedly higher percentage of males among Goldeneyes on a reservoir than on the neighbouring pot-holes. This was related to the fact that paired Goldeneyes left the reservoir, leaving unpaired

Table IX. Percentage of adult males among Goldeneyes, *Bucephala clangula*, on lakes in SW Scania in 1961–68 and on inland localities north of Scania at the wildfowl counts in 1959/60–1964/65. Numbers counted in brackets

Month	Lakes in Scania	Wildfowl counts
Oct.	15.6 (334)	29.8 (956)
Nov.	29.3 (985)	50.0 (913)
Dec.	34.6 (168)	51.3 (435)
Jan.	57.0 (37)	57.7 (1134)
Feb.	69.6 (83)	57.3 (366)
March	55.5 (1058)	58.0 (1071)
April	45.6 (1057)	57.4 (3914)
May	25.9 (54)	42.7 (450)

birds and surplus males behind. In Scania the percentage of paired Goldeneyes was higher on inland lakes than on the coasts (Nilsson 1969a). Differences in habitat preferences between the sexes of the Goldeneye were also reported by Lebreton (1961).

The percentages of males in flocks of different sizes were also established. In the shallow areas of the Öresund study area, no clear tendency was found, but on the south coast males were relatively more common in the larger flocks (Table VIII).

On the lakes in southwest Scania, the percentage of males was generally higher than on the coasts (Table IX).

On the river Göta älv at Trollhättan, adult males were rare during the early winter (Nilsson 1967). From January onwards, a marked male

Table X. Percentage of adult males among Goldeneyes, *Bucephala clangula*, in different regions at the wildfowl counts in Sweden during January 1966–1969. Numbers counted in brackets

Region	1966	1967	1968	1969
Scania south coast	55.2 (2150)	50.7 (2717)	—	—
Scania Öresund coast				
Klagshamn–Landskrona	40.0 (1175)	38.4 (1641)	—	—
Landskrona–Mölle	61.6 (1574)	51.3 (667)	50.9 (823)	52.7 (633)
Halland coast	73.5 (238)	71.8 (333)	—	—
Öland coast	38.2 (186)	—	—	48.2 (880)
Blekinge coast	—	—	—	29.4 (567)
Gotland coast	—	—	52.5 (267)	60.5 (532)
Inland localities	—	54.9 (225)	52.8 (182)	56.8 (356)

predominance was found, but the percentage of males decreased during spring migration. At Hallsjön, Trollhättan, the percentage of adult males decreased during spring migration, and immature birds followed late in the season.

Data on the percentage of adult males were also obtained from the wildfowl counts (Table IX). In October–November and in May some immature ducks might have been included among the females, but in the winter the values represent total of males. No differences were found between years and localities for the inland areas, but in the counts from January marked differences were found between different coastal regions and between the coast and inland (Table X). In autumn and spring, adult males were relatively more common on inland localities north of Scania than in Scania itself (Table IX).

Sex-ratio data on the Goldeneye from various parts of Europe were recorded by Bezzel (1959), Burckhardt (1958), Ehrlich (1963), Frieling (1934), Lebreton (1961), Linkola (1960), and Nilsson (1969b). Marked regional differences were found. Females and immature birds

Table XI. Percentage adult males among Eiders, *Somateria mollissima*, on the coasts of Scania in 1964/65–1967/68. Numbers counted in brackets

Month	Öresund	South coast	NW Scania
Sept.	3.6 (334)	3.7 (54)	—
Oct.	5.4 (259)	3.1 (161)	—
Nov.	2.5 (906)	1.6 (312)	—
Dec.	0.9 (574)	3.1 (383)	—
Jan.	1.9 (463)	4.6 (283)	29.2 (280)
Feb.	4.4 (586)	5.6 (303)	—
March	4.2 (452)	8.9 (291)	—
April	46.6 (1249)	36.0 (294)	—

migrate further to the south than the adult males, who were found to dominate most winter quarters in Sweden north of Scania and in some parts of north Germany, whereas females and first-winter birds were in majority in most other areas.

Long-tailed Duck, *Clangula hyemalis* (L.)

The counts from the south coast in all years showed a marked male predominance that decreased as the season proceeded (Fig. 5). In Schleswig-Holstein, Schmidt (1966) found a similar pattern. In the mild winter of 1966/67 the percentage of males was lower than in the other winters.

Eider, *Somateria mollissima* (L.)

Adult males were in a very marked minority on the coasts of Scania during the winter

Table XII. Percentage of adult males among Red-breasted Mergansers, *Mergus serrator*, on the coasts of Scania in 1964/65–1967/68. Numbers counted in brackets

Month	Öresund	South coast
Nov.	26.0 (181)	43.2 (555)
Dec.	40.6 (118)	57.6 (696)
Jan.	37.5 (64)	56.4 (681)
Feb.	50.0 (100)	59.2 (753)
March	51.1 (133)	52.5 (88)
April	59.0 (288)	58.2 (433)
May 1–15	52.1 (217)	—

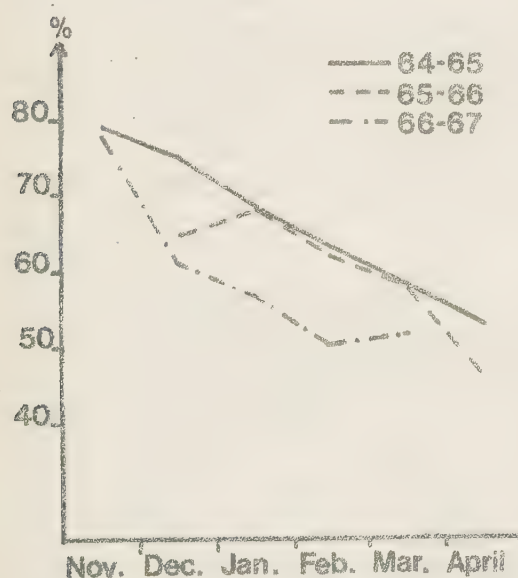


Fig. 5. Percentage of males among Long-tailed Ducks, *Clangula hyemalis*, in the south coast study area as monthly means from the counts in 1964/65–1966/67. Correlation coefficient for all years together -0.87 ($P < 0.001$).

Table XIII. Percentage of adult males among Goosanders, *Mergus merganser*, in the Öresund study area 1962/63–1966/67. Numbers counted in brackets

Month	1962/63	1963/64	1964/65	1965/66	1966/67
Nov.	—	—	—	51.4 (144)	—
Dec.	—	39.5 (76)	—	68.5 (111)	66.7 (33)
Jan.	64.7 (71)	69.5 (114)	56.7 (217)	76.9 (792)	64.7 (383)
Feb.	74.8 (571)	—	54.5 (788)	73.2 (809)	55.8 (314)
March	80.6 (211)	—	58.7 (537)	51.6 (120)	38.5 (52)
April	62.2 (119)	—	—	45.2 (31)	—

(Table XI). Immature males were somewhat more common, but were not regularly separated and thus not shown in the table. NW Scania, which lies nearer to the wintering areas of the Eider than the study areas in Öresund and on the south coast, had a higher percentage of adult males. During spring migration, a much higher percentage of adult males was noted.

Red-breasted Merganser, *Mergus serrator* L.

Percentages of adult males on the coasts of Scania are shown in Table XII. Högström (1966) found similar values at Gotland as those from the south coast of Scania, i.e. a slight dominance of males in the winter. On the coasts of Scania practically no immature birds were seen from January to April.

Table XIV. Percentage of adult males among Goosanders, *Mergus merganser*, in two study areas in Scania 1962–68 and at the wildfowl counts in Sweden north of Scania in 1959/60–January 1969. Numbers counted in brackets

Month	Scania		Wildfowl counts
	South coast	Inland lakes	
Oct.	—	16.4 (67)	35.0 (134)
Nov.	—	32.2 (806)	36.2 (526)
Dec.	59.0 (464)	44.2 (856)	51.8 (1044)
Jan.	59.3 (2954)	67.2 (258)	55.2 (4241)
Feb.	62.5 (2659)	62.9 (175)	54.0 (947)
March	53.5 (1331)	50.4 (2160)	57.3 (2038)
April	32.0 (243)	40.8 (1529)	51.0 (2172)

Goosander, *Mergus merganser* L.

Immature males could not be separated in the autumn and sometimes not in the winter and spring, so the values discussed are percentages of adult males. In the winter, few first-winter males were seen in normal winters, so the percentage of adult males will probably be almost the same as the percentage of total males for these winters.

Counts from the coasts of Scania showed a marked male predominance during the winter months (Tables XIII and XIV). In the two severe winters of 1963 and 1966, the percentage of males in the Öresund study area was markedly higher than in the other years. In most years no differences were found between the two study areas, but in January and February 1966, the Öresund had a significantly higher percentage of adult males than the south coast.

Table XV. Percentage of males among Smews, *Mergus albellus*, in SW Scania 1961–68 and at the wildfowl counts in Sweden during 1959/60–January 1969. Numbers counted in brackets

Month	SW Scania		Wildfowl counts
	Öresund	Inland waters	
Nov.	—	16.2 (74)	—
Dec.	47.5 (236)	22.7 (119)	38.0 (92)
Jan.	48.8 (425)	51.4 (72)	55.2 (437)
Feb.	58.0 (510)	47.8 (44)	57.4 (94)
March	50.9 (610)	49.1 (181)	49.1 (114)
April	45.4 (75)	48.0 (171)	48.2 (110)

Counts on the lakes in Scania differed somewhat from the counts obtained at the coasts (Table XIV). In December, females predominated on the lakes whereas males predominated on the coasts. In January, males were predominant in both areas but more markedly on the lakes than on the south coast. In the wildfowl count data, a slight predominance of males was found for all months except October and November (Table XIV). No differences were found between areas and years in this material except that the coasts of Blekinge in January 1969 only had 31.6 % males (752 counted); these counts were accordingly not included in the table. In March and April the wildfowl count localities had a higher percentage of adult males than the lakes in Scania, showing that spring migration is initiated by the adult males.

At Trollhättan, the river Göta älv had a moderate male predominance all through the winter. In spring, this area had a higher percentage of adult males than Lake Hallsjön, where many immature birds were counted (Nilsson 1965).

Bezzel (1959) found that the majority of females and immature birds migrate and winter further to the south than the majority of the adult males. Linkola (1960) and Hildén (1964) found a slight preponderance of males upon their arrival in Finland.

Smew, *Mergus albellus* L.

The data indicate an equal sex-ratio or a slight predominance of males on the coasts of Scania and other areas in south Sweden during the winter (Table XV). According to Bezzel (1965) and Ehrlich (1963) females clearly predominate among Smeews wintering in Germany.

CONCLUSIONS

The observed sex-ratios discussed in this paper are the results of various influences on the basic sex-ratios of the populations. The factors that influence the sex-ratios (counting errors excluded) may be grouped as follows: (1) different flocking tendencies of the sexes, (2) dif-

ferent habitat preferences of the sexes, and (3) differential sex and age migration resulting in seasonal and regional variation in the sex-ratio.

A marked variation in the percentages of males was found between flocks of varying sizes in the Tufted Duck and Goldeneye, with males being more common in the larger flocks.

Sex-ratio differences between habitats were found in the Tufted Duck and Goldeneye. In the Goldeneye they are possibly related to larger food requirements of the females making it necessary for them to feed in shallower water than the males (Nilsson 1970).

Differential sex migration was found in all species studied except the Red-breasted Merganser, for which data were obtained from only one area.

In the Tufted Duck, the males began their migration south somewhat earlier, probably owing to their earlier moult. In the Pochard, Bezzel (1959) was able to demonstrate the same pattern in Germany, but the Swedish data are probably too few. In spring, migration was initiated by males in both species.

The Scaup had a different seasonal pattern from all other species studied. Females were in marked predominance all through the winter but the proportion of males increased as the season proceeded.

In the Goldeneye, Goosander, and Smew, females and immature ducks initiated autumn migration followed by the adult males, who stayed further to the north than the females and immatures. From these species in Sweden, almost no immature birds were seen in the winter. Spring migration was initiated by adult males.

The Long-tailed Duck had another seasonal pattern with a marked dominance for males during the early season and almost equal sex-ratio during the spring.

In the Eider, finally, very few adult males were seen in the winter.

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